Paleontology - Ancient Marine Reptiles

Content:

Introduction To Marine Reptile Diversity

1 Adaptations Of Aquatic Tetrapods

Hello, my name is Scott Persons. I am a paleontologist at the **University of Alberta**. Let me welcome you to our course on marine Reptiles.

Life on Earth began in the Oceans more than 3,500,000,000 y ago, meaning that you, every living thing, and I are a descendant of a marine organism. Then, around 380,000,000 to 400,000,000 y ago, a few brave fish-like creatures made the transition from sea to land, and became the first terrestrial vertebrates.

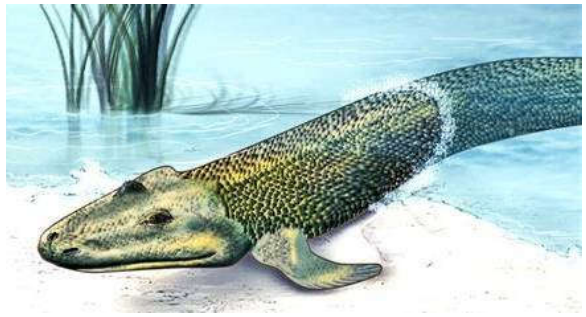
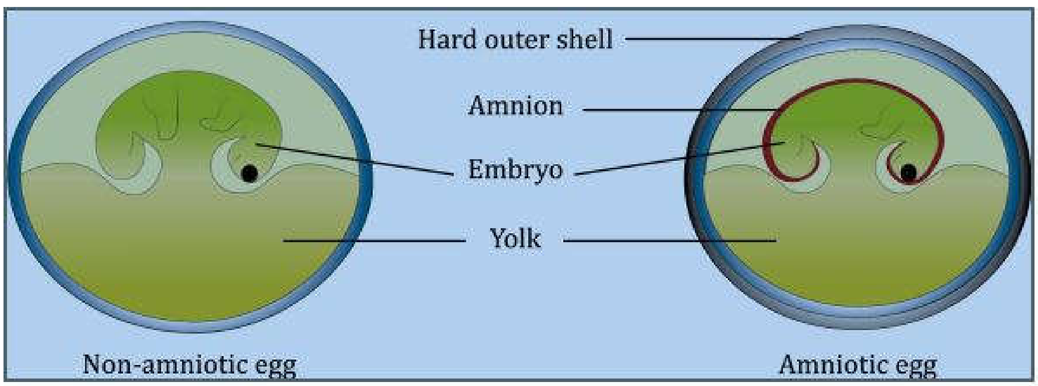


Illustration 1: ***Tiktaalik (Life reconstruction)***

These animals were the first Tetrapods, which were named for their four feet. One example of an early Tetrapod is *Tiktaalik*.



As Tetrapods evolved adaptations for life on land, one lineage, called Amniotes, evolved an extra protective layer around their embryos called an Amnion, which protected the developing young from drying out. This allowed Amniotes to lay eggs on dry land and completely cut their ties to the water. Amniotes continue to develop specializations for living on land and diversify to fill in an amazing array of terrestrial habitats. Interestingly, it was not long before some of these terrestrial Amniotes once again embraced an aquatic lifestyle. We will never know for certain why they returned to the Oceans. They may have been searching for more abundant food sources or could have been avoiding predators. The only thing the Fossil evidence shows with certainty is that they did leave the land and returned to the water.

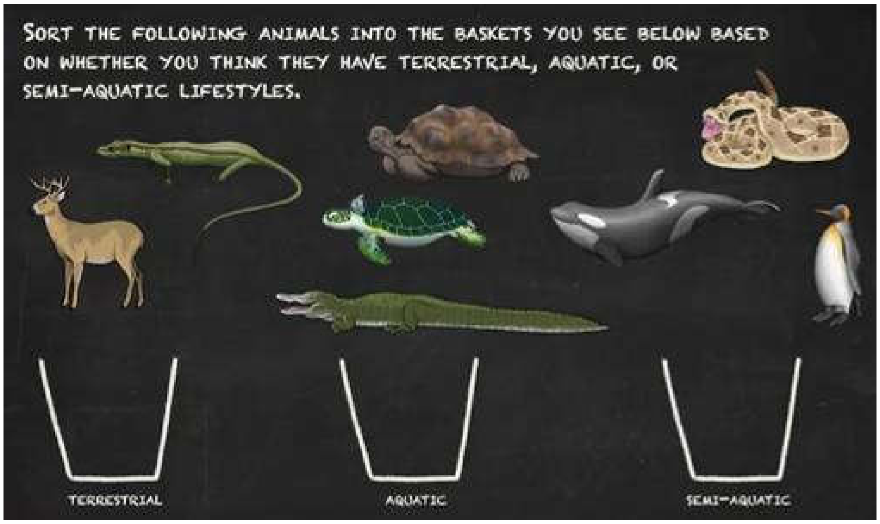
What happens when a terrestrial amniote returns to the water permanently? How do air breathing, landlubbing Amniotes once again adapt to life in the sea?

We can see that throughout the course of evolutionary history, many terrestrial Amniotes have returned to the water. In fact, many examples of them are living today, including Whales, Seals, Crocodiles, Sea turtles, and Penguins. Each of these animals had ancestors that returned to the water and faced new challenges in their aquatic environment. The process of overcoming these challenges, what we refer to as the aquatic problem, is the main theme of this course. Over the lessons of this marine reptile's course, I will introduce you to some of the Amniotes that made the transition back to aquatic habitats, and the ways in which they solved the aquatic problem.

To understand the information in this course, you need to know how to read a phylogenetic tree, how the Fossil record is interpreted, and the basics of evolutionary biology and comparative anatomy. If you are feeling a bit rusty on any of these topics, you might want to review your notes from an introductory biology or geology course for a refresher.

Before we get started, let us explore your ideas on one of the most fundamental concepts we will be discussing in this course, the general morphology, or body shape and structure, of an amniote that has returned to the sea.

1.1 Terrestrial, Aquatic, And Semi-aquatic



All the animals you just sorted are Amniotes that have adapted to different habitats and lifestyles. The Deer, Snake, Lizard, and Tortoise are all terrestrial. These animals might be able to swim, if they are forced to go in the water, but would be perfectly happy to spend their entire lives on land.

The Orca is the only one of these Amniotes that is aquatic, meaning that everything it needs for all aspects of its life can be found in the water. Crocodile, Sea Turtle, and Penguin are all semi-aquatic, and need both the land and the water to survive.

In the previous exercise, we looked at semi-aquatic lifestyles, but it is important to note that there is a full spectrum of semi-aquaticness. On one end are animals like Penguins that only go into the water to hunt for food, on the other end of the spectrum are animals like the Leatherback Sea Turtle that spend nearly its entire life at sea. In fact, female Leatherback Sea turtles only come ashore one day a year to lay eggs. Males never return to shore after they hatch. Even though Sea turtles spend so much of their lives in an aquatic setting, they are still considered semi-aquatic, because without that one tie to land, they would go extinct. Fish, on the other hand, are aquatic. Since all living Fishes descended from ancestors that were also aquatic, we consider Fish as primarily aquatic. Any semi-aquatic or fully-aquatic Amniotes are considered as secondarily aquatic, because they descended from ancestors that were terrestrial.

1.2 Extant Aquatic Reptiles

The purpose of this course is to understand the aquatic adaptations of Mesozoic Reptiles, but like all aspects of paleontology, our knowledge is based on modern life. Understanding the aquatic Reptiles of today will enable you to draw analogies between more familiar, modern organisms and the less familiar ones we will discuss later. Let us start with an overview of some aquatic Amniotes that live in the sea today.

When we think about secondarily aquatic animals, we normally think of Mammals, and several groups of Mammals live in the Ocean today. Whales and Dolphins are the most obvious, but there are also Seals, Sea Lions, Walruses, Sea Otters, and Manatees. Most of these animals have long, smooth bodies, flippers, a tail fluke, and no hind legs. This makes it very difficult, if not impossible, for them to move around on land. Other types of modern animals, like Penguins and Turtles, who spend their lives swimming and diving, are also secondarily aquatic Amniotes.

1.2.1 Aquatic Reptiles

Reptiles are not generally the first thing that you would think of if asked to name a secondarily aquatic animal. However, many Reptiles today are very successful in the marine environment.

Which of the following groups of Reptiles have aquatic members living today? Check all that apply.

A. Turtles

B. Snakes

C. Alligators and Crocodiles

D. Lizards

I was not kidding when I said that Reptiles were successful in the marine environment. All of these groups have members that live in and around the water today, therefore, all four answers are correct. Let us talk about some of these Reptiles.

1.2.1.1 Turtles

In this section, we are going to introduce you to a variety of aquatic Reptiles and some of the adaptations they have to living in water. Likely, the most familiar aquatic Reptiles alive today are Turtles.

Illustration 2: Hawksbill Sea turtle

Numerous Turtle species are secondarily adapted to an aquatic life, living in freshwater environments such as lakes and rivers. Sea turtles are adapted to saltwater environments, and spend their entire lives in the Ocean, venturing onto land only to lay eggs. Sea turtles tend to display a flatter, smoother body form than freshwater forms, and they have flippers instead of feet.

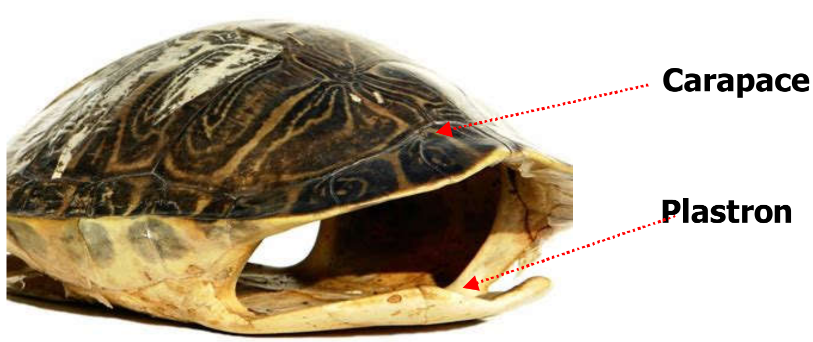


Illustration 3: Turtle shell

Now, all species of Turtles are characterized by a shell, made up of a dorsal carapace and a ventral plastron that encloses the body.

1.2.1.2 Crocodylomorpha

Illustration 4: American Crocodile

Alligators and Crocodiles belong to a group known as the Crocodylomorpha. They have long pointed heads, an elongate body covered with bony armor, webbed toes, and a powerful, laterally compressed tail. These Reptiles are generally large, reaching up to 12 m long. Crocodylomorpha are semi-aquatic, since they carry out important aspects of their lives on land and in the water. They live in and around shallow waters such as rivers, lakes, swamps, and streams. Today, only the Saltwater Crocodile has colonized the Ocean and can move far away from shore. Although they usually live in rivers, estuaries, and along the coast, they are known to use Ocean currents to move between Indonesian islands.

1.2.1.3 Snakes

Illustration 5: Yellow-lipped Sea Krait

Among Snakes, many extant, or currently living species, have adaptations to various fresh water and marine environments. These include swamps, rivers, coastlines, lagoons, and other shallow marine environments. Of the 62 living species of Sea Snakes, most live in shallow coastal waters, and can dive up to 100 m to find food near the bottom. All but one of these species bears live young, and all have a characteristically broad and paddle-like tail to help them swim. Many Sea Snakes have developed permeable skin to help them breathe, and adaptations in the lung and heart to facilitate long, deep dives.

1.2.1.4 Marine Iguana

Illustration 6: Marine Iguana

The Marine Iguana is one of the unique animals found on the Galapagos Islands. Although mostly terrestrial, it swims and dives in order to forage for its favorite food, algae. It mostly inhabits rocky shores, but it is also found in marshes and mangrove beaches. These large Lizards have developed adaptations for swimming, such as a laterally compressed tail.

The marine animals we just mentioned look very different from each other, even though their ancestors faced the same challenges and limitations as they transitioned from land to water.

What do you think are some differences between a terrestrial and an aquatic habitat that a secondarily aquatic amniote would have to adapt to? Check all that apply.

- **A.** Water creates higher drag than air
- **B.** Gravity does not exist in the water
- **C.** Animals walk on land, but have to swim in the water
- **D.** Animals living in water need gills to breathe instead of lungs

As aquatic Amniotes evolved, they all had to adapt to life in a different medium. This created interesting challenges that required major changes to their bodies in order to cope. Water is denser and more viscous than air, which causes more drag; therefore, **A** is correct.

Animals also have to evolve new ways to generate thrust, since most animals do not walk in the water; they swim. Therefore, **C** is also correct.

Gravity still exists in water even though it is counteracted by the force of buoyancy; therefore, B is incorrect. Finally, to breathe water an animal needs gills. However, it is *not* necessary to breathe water to live in water. All aquatic Amniotes still have lungs and breathe air; therefore, D is also incorrect.

The challenges we just discussed, and a number of other differences between air and water, combine to form the aquatic problem. The ancestors of secondarily aquatic animals were adapted to a terrestrial life; they breathed air and had legs.

How did they survive a transition to the aquatic environment and then go on to thrive in the water? What problems did they face and how did they overcome them?

In the next section, we will address several aspects of the aquatic problem, and give examples of how modern animals have adapted to solve them.

2 The Aquatic Problem

Before we move on, take a moment and try to think of some ways that humans artificially modify our bodies to be more efficient in the water.

What specific clothing or equipment do we use, and how would these modifications differ if someone is swimming laps in the pool or diving to explore a coral reef?

Humans have invented a number of tools that enable them to explore the aquatic environment. The use of scuba gear, goggles and wet suits, are some of the examples you may have thought of. Further examples will be introduced in this section, as we discuss some of the specific factors that contribute to the aquatic problem.

2.1 Propulsion: Moving In A Liquid

First, let us consider the differences in movement, on land as opposed to movement in the water. On land, your feet push against the ground to move forwards.

In water, against what do you push?

Some semi-aquatic Mammals, like Hippos, can walk along the bottom of lakes and rivers.

What is about animals that live out in the open Ocean?

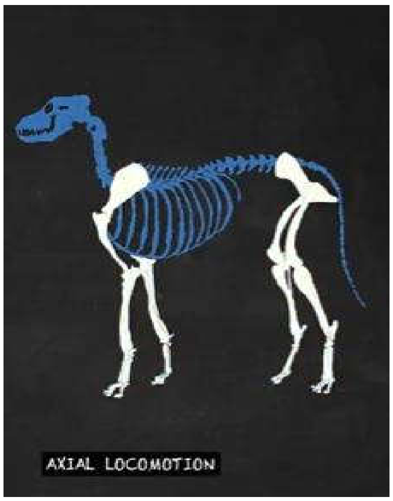
In order to move, they have to push against the water itself. Adapting to push against water instead of land is the first aspect of the aquatic problem we will address. If you move your hand through the air in front of you, you feel almost nothing. However, if you were to repeat that motion underwater, your hand would encounter a lot of resistance. This resistance results from the greater density of water, which is what Amniotes push against to generate propulsive force that moves them forwards. This is known as thrust.

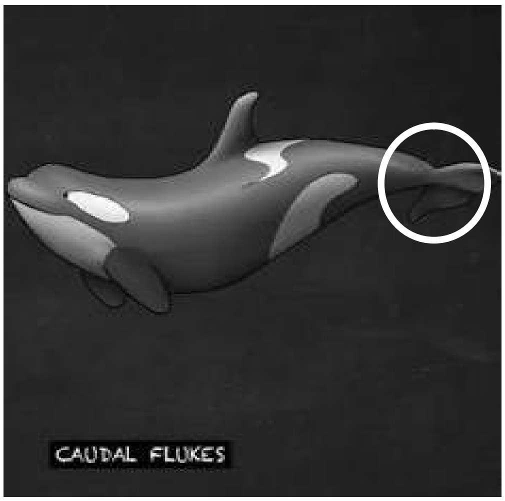
Some semi-aquatic Amniotes, like Ducks and Beavers, have webbing between their toes that increases their surface area. In this case, more surface area means that they push against more water, which results in more thrust. Next time you go swimming, try moving your hand through the water, first with your fingers spread apart, and then with your fingers pressed together. You generate much more thrust and movement with a closed hand than an open hand. You can generate even more with the aid of a swimming paddle. Human feet are not particularly efficient at displacing much water to generate thrust. Therefore, scuba divers can generate more thrust by wearing swim fins.

Illustration 7: Flipper (Humpback Whale)

Another adaptation to increased propulsion is the flipper. Almost all aquatic and semi-aquatic Amniotes have developed flippers, which are limbs adapted to generate thrust in water. Compared to a terrestrial limb, such your own hand, the bones in the flipper tend to be flatter than the humerus, radius and ulna are often proportionately shorter. On the other hand, the phalanges, or finger bones, are proportionately longer. Flippers are encased in tissue that makes a smooth, flat appearance like a wing. Flippers are not very good at supporting weight on land, although some Amniotes, like Sea Lions, retain some weight-bearing abilities in their front limbs. Others, like Penguins and Sea turtles, use their flippers like underwater wings to generate thrust.

2.1.1 Axial And Appendicular Swimming





Flippers are part of the appendicular skeleton, which includes the limb, hip, and shoulder bones. We say these animals move using appendicular locomotion. Axial locomotion is called when an animal generates thrust with its **axial skeleton**, which includes the head, spine, and tail. In order to generate more thrust from tail movement, Whales and Manatees have caudal flukes that increase the surface area of their tails. The caudal fluke sits at the end of the tail and is supported by the vertebrae. They are made out of concentrated bundles of dense, fibrous connective tissues called collagen.

Sea Snakes have also evolved a flattened, paddle-like fluke that increases the amount of thrust their tails generate as they undulate. These three animals are representative of the Fossil marine Reptiles we will focus in the following lessons. Based on what you have just learned about the parts of the body that can generate thrust:

Which of these three animals are axial swimmers?

A. Ichthyosaur

B. Plesiosaur

C. Mosasaur

The Plesiosaur has limbs that have been modified into large flippers, and not much of a tail fluke. Therefore, it is most likely an appendicular swimmer. The Ichthyosaur and Mosasaur have smaller flippers and more developed tails; therefore, it is more likely that they use axial locomotion. Therefore, **A** and **C** are the correct answers. Note how the tail of the Ichthyosaur and Mosasaur are completely different. The Ichthyosaurs tail is short and crescent shaped, and the Mosasaurs tail is long and broad. Even though both generate thrust using their exoskeleton, they did so in different ways.

The most common solution to the problem of underwater thrust generation is to use a high surface area flipper or fluke in a continuous motion. Think of the foot propelled swimmers such as a Duck, or the flipper propelled swimmers such as Sea turtles. Like a human swimmer doing freestyle, these animals move their limbs continuously in an efficient alternating pattern, which prevents them from slowing down. Animals that use axial locomotion, such as Sea Snakes and Whales, undulate continuously as they swim. Look at a swimmer doing a Dolphin kick. Humans use axial locomotion in this swimming style. You can see that the entire body undulates with the movement wave starting in the abdomen. There are three major types of axial locomotion in aquatic animals differentiated depending on where the wave starts in the body.

2.1.1.1 Anguilliform Locomotion

Anguilliform locomotion describes a motion where the propulsive wave originates at or near the head, and then ripples down the entire body. It is most obvious in Sea Snakes and Eels. Anguilliform swimmers tend to be very long and skinny.

2.1.1.2 Thunniform Locomotion

Thunniform locomotion is seen in several kinds of high-speed predatory Fish, like Tuna, and in some Dolphins. Thunniform swimmers begin their undulatory wave at or just in front of the fluke. Therefore, the body does not oscillate during swimming. We tend to see broad torpedo shaped bodies and crescent shaped fins and flukes in thunniform swimmers.

2.1.1.3 Carangiform Locomotion

In between these two extremes are carangiform swimmers. In this kind of locomotion, the angulatory wave starts somewhere in the back half of the animal, but not quite at the tail fluke. Seals, Crocodiles, and Marine Iguanas swim using this mode of locomotion.

What kind of swimming mode is being used by a Whale? As a hint, try to look at how much of the body ungulates.

A. Anguilliform

B. Carangiform

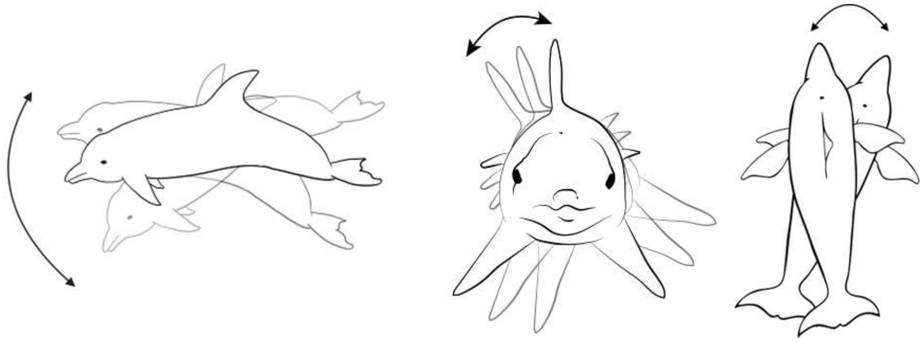
C. Thunniform

If you look at a Humpback Whale, you can see that only the back half of the body undulates. In Anguilliform swimmers, undulation starts at the neck. A is not correct. In thunniform swimmers, only the caudal fin or fluke is it that oscillates; therefore, C is not correct.

In carangiform swimmers, the undulatory wave starts in the back half of the animal, but still well before the caudal fluke or fin. Therefore, **B**, carangiform locomotion, is the correct answer.

2.2 Stability: Controlling Movement In A 3D-Environment

As we have already discussed, the high density of water allows aquatic animals to push against the water surrounding them in order to move. A terrestrial animal can push off the ground in four directions: forwards, backwards, left, and right. We can jump too, but since we always come back down, it does not really count as sustained directional movement. Being able to push off the surrounding water enables aquatic animals to move up and down at will. Terrestrial animals only move in two dimensions, but aquatic animals move in three. This means that aquatic animals have to be stable in three dimensions, instead of just two. This is the second aspect of our aquatic problem.



Pitch Roll Yaw

Illustration 8: Movement control of animals in water

If you ever played with a toy boat on the water, you know that it can be difficult to stop it from rolling over, and the problem just gets worse underwater, especially at high speeds.

An aquatic animal needs to be able to control their up-down and left-right motions and needs to be able to control how much they roll. Whales and Dolphins mostly use their flippers for maneuvering and stabilizing their body, so it does not roll sideways while moving forwards. Sea turtles are flat enough and slow enough that their bodies do not roll very easily. Some Whales and Dolphins have a prominent dorsal fin, which helps stabilize the body against rolling, especially those that typically move at great speeds. Think about steering a car or a bike. At low speeds, you have to use large motions to turn, but at high speeds, a small twitch of the steering wheel or handlebars has a much larger impact. Therefore, stability is more important for faster moving animals, which is why they tend to have larger dorsal fins.

2.3 Drag: Moving Through The Water

The high density of water also contributes to the third aspect of the aquatic problem we will discuss, the problem of drag. Imagine four swimming pools full of the following substances: honey, water, air, and cream.

Which would cause the least drag, and which would cause the most drag?

Drag resists the movement of our bodies through any medium, and it is increased by both higher density and viscosity. Air is much less dense than water and is less viscous. Moving through it causes less drag. Think about walking in a shallow swimming pool. The greater density and viscosity of water means it is much more difficult than walking on the sidewalk. Cream is denser and more viscous than both air and water, and honey is the densest and most viscous of all four. Therefore, the easiest substance to walk through is air, which causes the least drag followed by water, cream, and honey, which causes the most drag.

There are two types of drag that an animal experiences in the water, inertial drag and viscous drag. By combining, these two types of drag form the third aspect of the aquatic problem.

2.3.1 Inertial Drag

Inertial drag is caused by the high density of the water. As a body moves through water, it disturbs the water molecules, forcing the water to flow around it. Once the body has passed through the water, it leaves an empty space where the body used to be. Water enters this space, swirling, spinning, and creating turbulence. The empty space, which pulls the water in to fill it, also pulls on the object that created it. This causes inertial drag, sucking the object backwards. To minimize it, a body should be shaped so that it disturbs the water as little as possible as it passes through. Fewer disturbances mean less swirling water, less suction, and therefore, less wasted energy and decreased speed. An object that decreases inertial drag by minimizing disturbance to the water is described as streamlined.

Which of these bodied positions would be most streamlined in the water? Would it be a swimmer with his arms?

A. Held out sideways away from the body

B. Held against the side of the body

C. Extended out front above the head

Streamlining is easily visualized in the pool. When pushing from the wall, swimmers want to be as streamlined as possible so they can maintain maximum speed. Swimmers pushing off the wall with their arms wide and legs apart can barely move a meter before the significant inertial drag pulls them to a stop. With their arms held against their sides, they can move farther. However, if they stretch their arms straight out over their heads, keep their legs together, and their bodies straight, they can move several meters before their inertial drag slows them to a stop. Therefore, the most streamlined body position, and the correct answer is **C**.

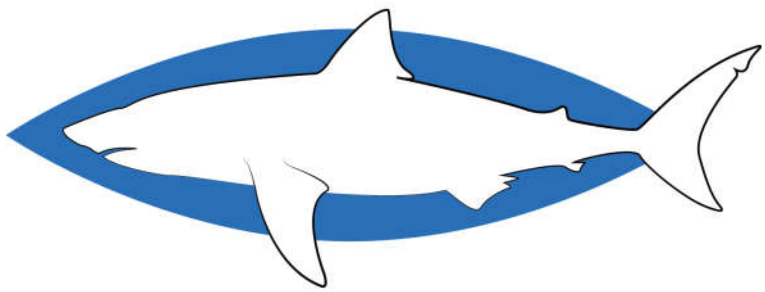


Illustration 9: Generalized fusiform shape (in blue) and as seen in a Shark (outline).

A well-streamlined body has a small amount of surface area in the direction they are moving resulting in a smooth, elongate shape. In the most derived cases, streamlining results in a smooth, torpedo-shaped body, referred to as fusiform. It can be seen in animals like Sharks, Tuna, and Dolphins. Different aquatic animals may be less elongate and smooth, but we tend to see some degree of streamlining in the body shape of Amniotes that spend a lot of time in the water.

2.3.2 Viscous Drag

The second type of drag is called viscous drag. Viscous drag is due to the higher viscosity of water. A highly viscous material resists flow, which causes a lot more friction as it moves over a surface and slows an animal down. To decrease viscous drag, the surface needs to be as smooth and frictionless as possible. Once again, let us picture this in a pool.

Swimmers wear tight fitting swimsuits and swim caps to cover their hair in order to minimize friction. Many Olympic swimmers even shave their legs and arms before racing. Whales and Manatees have lost all or most of their hair, resulting in smooth skin that produces much less drag. This allows them to swim using far less energy. Many marine Reptiles have smaller, smoother scales than their terrestrial relatives, which again, causes less friction, and therefore, less viscous drag. It is important to note here, that being surrounded by a high-density medium, such as water, does not just cause new locomotion problems for terrestrial Amniotes. It also confers a major benefit. On land, all of an animal's weight is carried by its feet, but in the Ocean, water supports the body on all sides. A terrestrial skeleton needs to be very strong and heavy to support an animal's weight, but in the water, a much smaller, more loosely attached skeleton can support a much larger body. This is why the Earth's largest animals are found in the Oceans.

2.4 Breathing: Returning To The Surface

Any Amniote that swims, including us, still needs to breathe air. No aquatic amniote has ever re-evolved gills or similar fish-like respiratory structures. This means that although locomotion and feeding occur in the water, they still must return to the surface to breathe.

How often? Which of these organisms can hold their breath underwater the longest?

A. Human

B. Sperm Whale

C. Emperor penguin

D. Saltwater Crocodile

The average human can probably hold their breath for up to a minute to dive underwater. Animals, like Crocodiles, Marine Iguanas, Penguins, and most Whales can go about 10 – 30 minutes between breaths. Sperm whales can hold their breath for about 90 minutes. That makes **B** the correct answer.

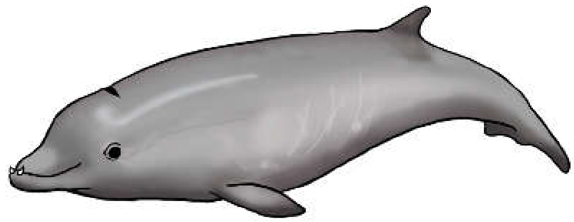


Illustration 10: Cuvier's Beaked Whale

Currently the record holder for longest dives is a Whale, you might not have heard of, called Cuvier's Beaked Whale. They can stay underwater without breathing for more than two hours.

How do these aquatic Amniotes manage to stay under water for such long periods?

Like us, all Amniotes have lungs, which mean they have to return to the surface periodically to breathe. This is the fourth aspect of the aquatic problem. Aquatic and semi-aquatic animals have evolved several different methods for dealing with breathing in aquatic environments. Crocodiles can tolerate much higher levels of Lactic acid in their blood, which is formed when Amniotes do strenuous activity without getting enough Oxygen. This is what happens when we run for a long time and get sore legs, or when we hold our breath while exercising. Whales take series of rapid breaths at the surface to supercharge their blood and muscles with Oxygen. Then, they use the Oxygen stored in their blood, rather than air in their lungs, to maintain their muscle activity during deep dives. Penguins slow their heart rate when they dive so that blood does not move around the body as fast, and the Oxygen is used slower. They also have an amazing ability to divert blood away from some organs and towards areas that are more critical when their Oxygen levels are depleted.

Illustration 11: Dog skull

Illustration 12: Beluga Whale skull

The need to surface for air also results in skull shape adaptations. In most terrestrial Amniotes, the nostrils, or nares, are located towards the tip of the snout, as you can see on this dog. In many aquatic Amniotes, the nares migrate towards the eyes, or the top of the head, so that the animal only has to lift a little bit of its body above the water in order to breath. This is easiest to see in Whales and Dolphins, like this Beluga Whale skull. In marine Mammals, these dorsally positioned nostrils are called the blowhole.

Illustration 13: Crocodile skull

However, this is not the case for every aquatic animal. For instance, Crocodiles' nares are on the tips of the snout, as you can see here.

2.5 Buoyancy: Trying not to float

Breathing air creates another problem for an aquatic amniote. Let us think again about our swimmer in the pool. Human bodies have about the same density as water. However, we also have a lot of air in our bodies, especially in our lungs, which cause us to float. Nevertheless, marine Amniotes do not want to float. They need to move up and down in the water easily, in order to find food.

2.5.1 Most Efficient Mass

What do you think is the most efficient mass for a secondarily aquatic animal? Remember that they need to be able to dive and surface with equal ease. A secondarily aquatic animal should have a mass that is.

A. Greater than the mass of water that their body displaces

B. Equal to the mass of water that their body displaces

C. Less than the mass of water that their water displaces

The correct answer is **B**. It is most efficient for a secondarily aquatic organism to achieve neutral buoyancy.

If something is neutrally buoyant, it will not float or sink when put in the water. It will stay exactly where it is. This means that the mass of the organism must be equal to the mass of the water that would otherwise occupy the same space. In other words, they must have the same density as the surrounding water. This is the reason that scuba divers wear weighted belts. It increases their mass so that they are neutrally buoyant.

Illustration 14: Manatee skeleton

Achieving neutral buoyancy is the fifth aspect of the aquatic problem. Aquatic Amniotes can solve it by increasing their body density, which is often accomplished by making bones heavier. For example, increasing the thickness of a bone makes it heavier. This is a condition we call **pachyostosis**. You can see it really clearly in this Manatee skeleton. Look how big the ribs are. These thick bones have a much higher mass than those of terrestrial animals, thus, increasing the animal's density and achieving neutral buoyancy. Pachyostotic bones are found in Manatees, Penguins, and some of the early relatives of Whales.

Illustration 15: Cross section of a pachyostotic, normal, and osteosclerotic limb bone from a CT-scan

Look at this cross section through a normal bone. If the outer layer of bone gets thicker, it is pachyostotic. Another way to make bones heavier is via osteosclerosis. This is where the bones stay the same size, but get much denser through the deposition of minerals in the inner cavities of the bone. This type of bone alteration is seen in Walruses and Turtles.

Crocodilians and some semi-aquatic Birds use a completely different method for maintaining neutral buoyancy in the water. These animals swallow stones, known as **Gastroliths**, in order to increase their mass. This additional mass within their stomachs increases the overall density of the animal's body, helping them achieve neutral buoyancy.

So far, in this lesson we have covered five aspects of the aquatic problem. Aspect one is propulsion or how Amniotes move through water. Aspect two is living in a 3D-environment instead of a 2D-environment. Aspect three is the drag they experience in the water. The fourth aspect is still the need to breathe air in their aquatic environment. In addition, the fifth aspect is buoyancy. Now let us continue.

2.6 Balancing Salt And Water: Fighting Osmosis

Breathing is also related to the sixth aspect of the aquatic problem. Excreting salt and obtaining fresh water in an environment made up of nothing but salt water. Breathing, like many other internal processes, produces water as a by-product. Amniotes lose a great deal of water through regular body processes, such as breathing and urination. Therefore, they either need to drink water directly to replenish lost fluids or absorb water from their food. However, they need to consume fresh water, not salt water. Even though salt is an essential mineral for their bodies, the concentration in salt water is too high for most animals to process and excrete. Too much salt throws off the balance of water in cells, leading to dehydration and death.

2.6.1 Cells In Seawater

What do you think happens to an animal's cells placed in a seawater solution?

A. The cell will shrink

B. The cell will expand

C. The cell will shrink, then expand, and then shrink again

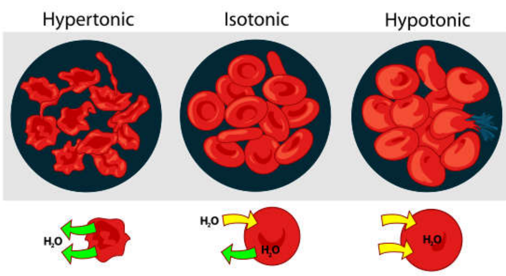


Illustration 16: Osmosis

Liquids on either side of a permeable membrane, like a cell membrane, are subject to **osmosis**. This is where water diffuses across the barrier in an attempt to equalize the balance of water to the environment. The average cell only has a tiny amount of salt in it. Therefore, if it is put into a very salty solution the water in the cell will rush out in an attempt to equalize the salt concentration between the two environments. Now, since water leaves the cell, the cell will decrease in volume and shrink. This means **A** is the correct answer.

This is why it is dangerous to drink salt water, because each cell loses water and dehydrates. In fresh water, the cell would expand as more water is drawn into the cell to equalize the environments, so B is incorrect. A cell would only shrink, expand, and shrink again in a fluid where salinity fluctuates. Therefore, C is also incorrect.

How do Amniotes that live in the Ocean replenish the fluids lost through breathing and urination without having access to fresh water?

The water they need mostly comes from the Fish and other animals they are eating, but some seawater is swallowed too. These animals have special adaptations that enable them to process safely the extra salt they ingest. Marine Mammals are able to concentrate and excrete the salt in their urine at much higher levels than most terrestrial Mammals.

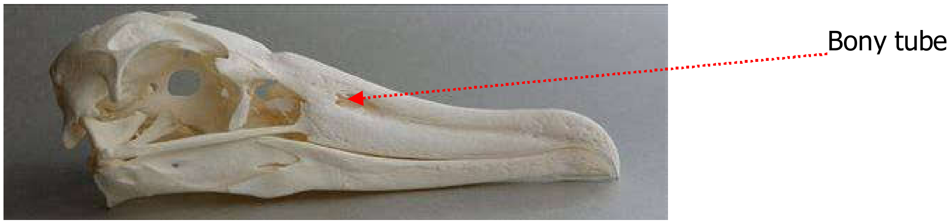


Illustration 17: Albatros skull

Sea turtles, marine Iguanas, saltwater Crocodiles, Penguins, and some Seabirds have independently evolved a special salt gland in their heads. These glands concentrate salt from the blood so that can be expelled in drips of water. In the saltwater Crocodile, the salt glands are found on the tongue, in Sea Snakes, they are under the tongue, and in Sea turtles and Birds, the glands are above the eyes and drain on to the surface of the eye or through the nose. This is why it looks, as if they are crying. They are actually expelling extra salt from their bodies. If you look closely at this albatross skull, you can see a small, bony tube. This tube is where the concentrated tears from the salt gland drain out onto the bird's face.

Marine Iguanas have salt glands above their eyes that are connected to their nostrils, and they forcibly remove the salt from their salt glands by sneezing. The spray often lands on their heads, leaving a crust of white salt on their faces.

2.7 Staying Warm: Maintaining Body Temperature

The problems of breathing, drinking and maintaining a salt balance all fall under the topic of metabolism, which is the sum of all the chemical processes that occur within an organism to maintain life. Like all chemical reactions, those that make up an organism's metabolism are affected by temperature. Most of the chemical reactions in our bodies can only take place within a very small temperature range, which is why hypothermia and heat stroke can easily be fatal.

2.7.1 Hypothetical Hypothermia

In which situation would you get hypothermia the fastest resulting in your body's functions slowing and stopping?

A. Standing in a 0 °C freezer

B. Sitting in the snow at 0 °C

C. Up to your neck in 0 °C water

The problem with water is that it is a very good conductor. It moves heat 24 times as fast as air. This means, that in water you would get cold 24 times as fast, and you are in 24 times as much danger of getting hypothermia. Therefore, you would get hypothermia slowest in the dry freezer, faster in the damp snow, and fastest when submerged in water; therefore, answer **C** is correct. This is why swimmers and divers wear wetsuits if they will be in the water for an extended time. The wetsuits slow heat conduction away from the body, allowing them to maintain their internal heat for longer.

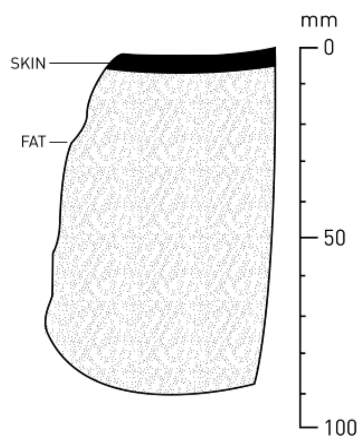


Illustration 18: Thickness of skin in comparison to blubber

This illustrates the seventh aspect of the aquatic problem, the higher heat conductivity of water. Marine Amniotes must either develop adaptations to stay warm or adapt their metabolism to cold-water temperatures. Mammals and Birds generate heat internally, and they have adaptations to stop their heat from escaping their bodies. Whales and Seals have a thick layer of fat called **blubber** to keep in heat. Other Mammals, like Polar Bears, the Platypus, and Otters, have fur so thick that water cannot penetrate through to their skin. Birds have water-repelling oil that coats their feathers and a thick layer of down feathers against their skin to keep them warm and dry.

Reptiles do not generate their own body heat. While their metabolism works well in warm temperatures, it is slower when they are cold. It is for this reasons that most modern aquatic or semi-aquatic Reptiles live in warm tropical waters. Sea turtles can be found in colder waters as far north as the Arctic, and they have become adapted to a slow metabolism.

2.8 Senses: Maintaining Sight And Hearing Underwater

The last aspect of the aquatic problem we will address in this course is the problem of the senses. If you have ever stuck your head underwater, you may have noticed that things sound weird, and everything looks blurry. Water affects light and sound much differently than air. The ability to sense accurately your environment is critical to survival, and secondarily aquatic animals have developed special adaptations as a result.

2.8.1 Sight

Let us first consider sight. The properties of water affect how light behaves in three main ways.

1. As light passes through a medium, such as air or water, the specific density changes how much light bends as it moves. The greater density of water causes light to bend less than it would in air. Our eyes, which are adapted to focus in air, cannot compensate. Putting on a pair of goggles creates a layer of air over our eyes that enable us to focus again. However, the different bending of light still results in objects appearing magnified by about 25 %.
2. Light is absorbed by water molecules and scattered by suspended particles. This means that light does not travel as far as it does in air, resulting in a reduced visual range.
3. Water acts as a filter, stripping away greater portions of the visible spectrum of light with increasing depth. Warm colors, like red and orange, barely penetrate the water at all, while greens and blues penetrate deepest. Only 50 % of light is able to penetrate up to 10 m, only 12.5 % by 30 m, and by 200 m, there is total darkness. That is in very clear water, it is even worse if the water is cloudy.

Since vision is so different in water, it makes sense that eyes are one of the things that show the most profound adaptations in secondarily aquatic animals. Many of these animals have proportionately larger eyes than their terrestrial relatives, which allow them to pick up more of the limited amount of light that penetrates through the water. The lens of the eye is also enlarged and almost spherical, adapted for focusing on light that bends as it enters the water. Often aquatic Amniote eyes contain high numbers of rod cells, which are the photoreceptor cells that are most sensitive to low light levels. Another common modification is the development of a lining on the back of the eyes called the *Tapetum lucidum*.

2.8.1.1 Tapetum lucidum

Have you ever noticed how a cat's eyes glow in the dark?

Illustration 19: The *Tapetum lucidum* reflecting light

This is because the *Tapetum lucidum* acts like a mirror reflecting incoming light back through the retina a second time, increasing the light gathering ability of the rod cells even in low light conditions. This adaptation is seen in semi-aquatic Amniotes such as Seals and Crocodilians.

2.8.2 Hearing

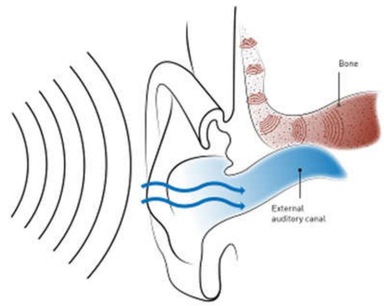


Illustration 20: Mammal acoustical system (Schematic)

Sound entering the external auditory canal creating sound waves in the bone (bone conduction). Blue arrows indicate the path of sound waves travel through the air-filled ear canal of terrestrial Amniotes. Red waves indicate the path the sound waves travel through bone conduction in aquatic Amniotes

Let us now consider an animal's hearing. Hearing underwater, unlike sight, actually functions better than it does on land. Sound travels more efficiently through higher density mediums, traveling much farther and up to five times faster in seawater than in the air. On land, sound vibrations strike the Amniote eardrum through an air-filled outer ear canal, but when a typical land animal is submerged in the water, water fills the ear canal, decreasing the ability to hear.

Underwater, it is much more common to pick up sounds through the skull bones, a phenomenon called bone conduction. When humans are underwater, this is actually how we hear, since our terrestrial ears are useless. This also explains why aquatic animals do not generally have external ears. They are unnecessary for bone conduction and only cause extra drag.

Whales live underwater and hear primarily by bone conduction. Bats fly in the air and hear using the typical mammalian air-filled ear system. Both have highly developed senses of hearing that they use to hunt. The two pictures shown here are diagrams showing the inner ear bones from a bat and a Whale.

Animals that live on land typically have thinner, more delicate ear structures that are well-adapted for picking up sounds in the air. In bats, the bones of the inner ear are especially thin and attached loosely to the skull to minimize the amount of bone conduction. This protects the bat from deafening itself while emitting high frequency sounds. Animals that live in water, like Whales, typically have thicker ear bones that are better at transmitting sound through the skull bones without distortion.

2.8.2.1 Echolocation

Because sound is such an effective sense underwater, many secondarily aquatic Amniotes have developed adaptations to take advantage of it. The evolution of large, bony plates in the ear facilitates the detection of sound and allows sound transmission to the inner ear with less distortion, and the ability to detect direction. Marine animals rely on sound to sense their surroundings, communicate, locate food and protect themselves.

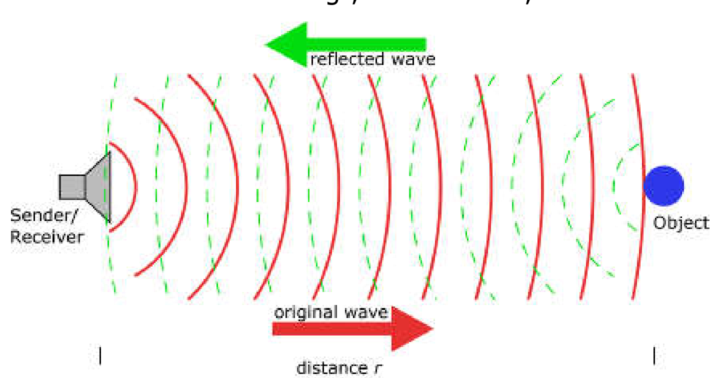


Illustration 21: Echolocation

Echolocation is an adaptation developed by some marine Mammals, such as Dolphins. They use a sonar-like system where the animal emit high pitch sounds that bounce off of surrounding objects, and are reflected back to the animal's ears. They are able to use the timing and pitch of the returning sound to identify the objects, such as food, obstacles, and other individuals.

2.9 Conclusion

As we have seen, there are a number of challenges faced by secondarily aquatic Amniotes, which affect various aspects of their ecology, which is the relationship of the organism with its surroundings. Modifications included alterations of the body to reduce drag, and adaptations of the limbs and tails in order to generate forward propulsion. Sensory structures changed and breathing structures adapted, but all secondarily aquatic Amniotes retain their air-breathing lungs. Though aquatic Amniotes have dealt with these challenges in a variety of ways, the fact that they all faced the same challenges means that many evolved similar or indistinguishable solutions. This is known as convergence. We will see this pattern repeatedly when we discuss paleoecology, or the ecology of extinct groups, throughout this course.

3 Classifying Aquatic Amniotes

3.1 Extinct Aquatic Amniotes From Less Diverse Or Short-Lived Clades

The focus of the remainder of this course is to explore how secondarily aquatic Amniotes survived and solved the aquatic problem by learning about the giant Reptiles that lived in the sea during the Mesozoic. This Era is composed of the Triassic, Jurassic, and the Cretaceous Periods when the Dinosaurs lived on the land and the Pterosaurs soared through the air.

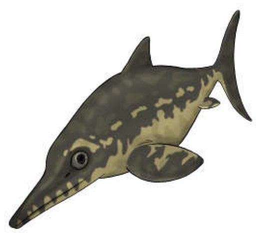


Illustration 22: Example of an Ichthyopterygian

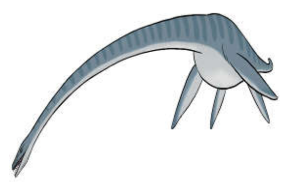


Illustration 23: Example of a Sauropterygian

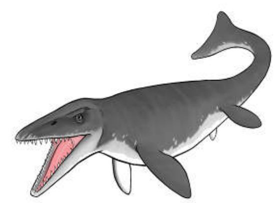


Illustration 24: Example of a Mosasauroid

Even if you do not know their names, you may have seen pictures of the Ichthyopterygians, the Sauropterygians, and Mosasauroids. These three groups are the most successful extinct marine reptile clades, or groups, of closely related organisms that all descended from a common ancestor. For each of these clades, we will focus on the evolution of aquatic adaptations within the group. We will start by introducing the basal, or earliest members, who had a few of the specialized aquatic adaptations seen in later, more derived members of the group. On your phylogeny tree, the basal members you always find near the base of that group's branch. The derived members you find on the ends of the branches.

The more derived members of each clade of marine Reptiles had flippers instead of feet, as well as a number of other adaptations to solve the various aspects of the aquatic problem. The next three lessons will examine these three groups in detail, but first we will learn a little bit about more obscure, extinct marine Reptiles that existed in the deep past, and some of the ways that they solve the aquatic problem.

3.1.1 Review Of Amniote Phylogeny

In order to put these clades in context, let us first review the phylogeny of the Amniotes. Amniote Tetrapods are the four-limbed vertebrates whose eggs have specialized membranes that maintain a constant internal environment for the developing embryo. Amniote evolution produced two major groups. These groups you can recognize by the number of holes in their skulls behind their eyes. We call these holes the temporal fenestrae.

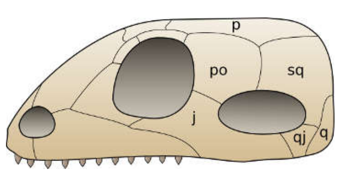


Illustration 25: Synapsid skull

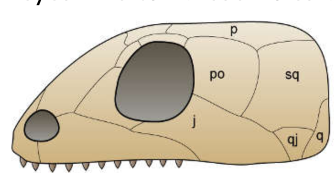


Illustration 26: Anapsid skull

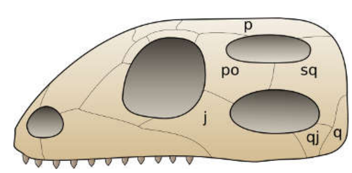


Illustration 27: Diapsid skull

The first of these groups is the Synapsida, which include the Mammals. All synapsids have only one temporal fenestra behind the orbit, as you can see above. The second group is the Sauropsida, and this clade includes the Parareptiles that show the Anapsid skull condition with no extra openings behind the orbit, as you can see above, called Labidosaurs. The other clade within the Sauropsida is Diapsida. Now these animals have two openings, called the laterotemporal and supratemporal fenestrae, which above you can also see.

The Diapsids are the most diverse group, include Birds, Crocodiles, and Lizards, all of which have two temporal fenestra. Living Diapsids are included within two clades, the Archosauromorpha, known as the ruling Reptiles, have an additional fenestrae in front of the eye and on the lower jaw. Lepidosauromorpha, or the scaly Reptiles, lack those openings. Birds and Crocodiles are the living members of the Archosauromorpha, but this group used to be much more diverse. Extinct members include the Dinosaurs, Pterosaurs, and many relatives of today's Crocodilians. Living members of the Lepidosauromorpha include Snakes and Lizards, but this group also includes many extinct forms.

3.1.2 Extinct Marine Reptile Groups

Let us take a closer look at some of the more obscure, extinct aquatic Amniotes. We will start with a first group of Reptiles known to have returned to an aquatic habitat.

3.1.2.1 Mesosaurs

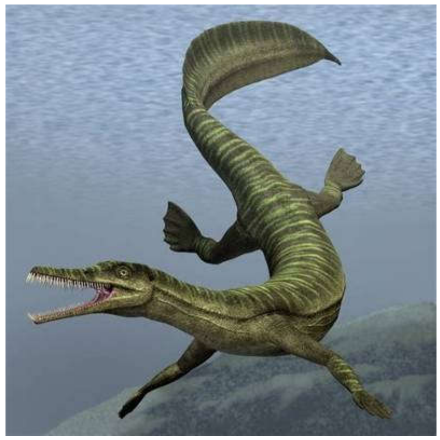


Illustration 28: *Mesosaurus* (Life restoration)

The first Tetrapods colonized the land during the Devonian Period, about 395,000,000 y ago. Less than 100,000,000 y later, during the Permian Period, the Parareptiles, known as Mesosaurs, reinvaded the water. Just do not confuse them with the Mosasaurs that are the focus of lesson four.

Mesosaurs were small Parareptiles, up to 1 m long, which had various adaptations for an aquatic life. They had a slender body, an elongate skull, and a long neck, which were perfect for streamlining and decreasing drag. Dense bones would have helped achieve neutral buoyancy, and the long hind limbs and a laterally compressed tail were probably used for propulsion. They also had long snouts with many small needle-like teeth that would have been good for grabbing Fish and other slippery aquatic prey. Mesosaurs were probably well suited to paddling in shallow coastal waters, but their lack of more specialized aquatic adaptations would have prevented their survival in the open Ocean.

3.1.2.2 Crocodylomorpha

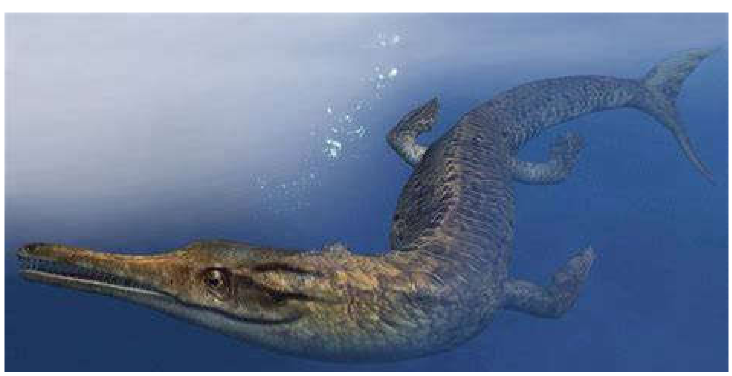


Illustration 29: *Geosaurus* (Life restoration)

Another group of semi aquatic Reptiles that might be familiar to you is Crocodylomorpha. All extant Crocodilians have aquatic adaptations like webbed feet and a powerful, laterally compressed tail. Some, like the saltwater Crocodile, spend a lot of time in marine habitats, but they are not adapted to life exclusively in water. However, in the Jurassic and Cretaceous, one extinct lineage of Crocodylomorphs, called the Thalattosuchia, evolved some marine species with some impressive marine adaptations.

3.1.2.2.1 Thalattosuchia's Adaptation

Based on this picture of a modern Crocodile and this reconstruction of a Thalattosuchian, try to identify some of the aquatic problems that the Thalattosuchians were better adapted to solve than modern Crocodiles. Check all that apply.

A. Adaptations for propulsion

B. Adaptations to facilitate air breathing

C. Adaptations to reduce drag

D. Adaptations to improve sight

Thalattosuchians had paddle-like forelimbs and a tail fluke. These adaptations would have helped it control its position in the water column and generate propulsion. Therefore, **A** is correct.

Thalattosuchian bodies were similarly shaped to modern Crocodiles and the nares are in the same place; therefore, B and C are incorrect. We also see no evidence of significantly larger eyes. Therefore, D is also incorrect.

There is some amazing evidence for salt glands in some Thalattosuchians. Natural casts of a lobe structure were preserved in the orbit of one Thalattosuchian specimen, and these structures are the right shape and in the right position to represent the salt glands. These animals must have been primarily marine, perhaps only venturing onto land to lay eggs.

Let us move on to some less familiar clades, which, like the Mesosaurs, have no close living relatives today. One of the most basal clades of the Archosauromorphs is called the Protorosauria, and it includes two clades of aquatic species.

3.1.2.3 Tanystropheidae

Illustration 30: *Tanystropheus* (Life restoration)

Tanystropheus, which belongs to the Tanystropheidae, is often reconstructed as an aquatic reptile. However, it lacks some of the specializations we would expect to see. It's limbs are not modified into paddles, and it's tail is not long, or laterally compressed. Tanystropheus is notable for it is extremely long and stiff neck, which it may have used to snatch Fish while sitting on the edges of lakes.

Another Tanystrophid, Dinocephalosaurus, also had a long neck, and it does have some of the features we would expect to see in an animal that spends most of its time swimming, including legs that are clearly modified into paddles. Therefore, at least some Tanystrophids spend most of their lives in the water.

3.1.2.4 Drepanosauridae

Illustration 31: *Hypuronector* (Life restoration)

Another clade of Protorosaurs, the Drepanosaurs, are some of the strangest of the extinct Archosaurs. They seem to have been, somewhat, convergent on modern day Chameleons. They had grasping feet and hands that would have made them proficient tree climbers, and huge claws that might have been good for digging or ripping through bark. However, one Drepranosaur, Hypuronector, has a very tall, laterally compressed tail that resembles the tail of a newt. Some paleontologists have argued that this morphology probably would not be very practical for maneuvering through tree branches, but would have been useful for generating thrust in the water. Hypuronector is more abundant than other Reptiles in the lake deposits where it is found.

3.1.2.5 Choristoderes

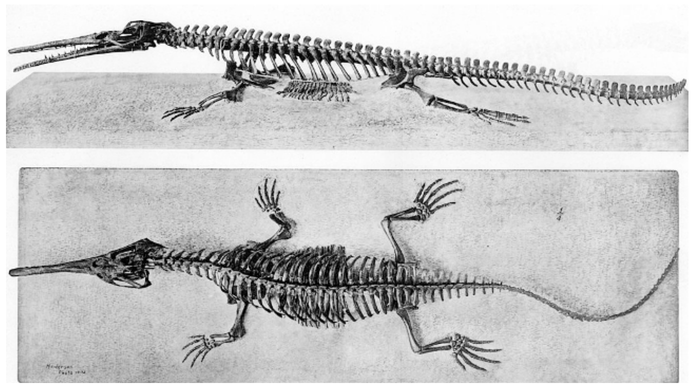


Illustration 32: *Champsosaurus* (Fossil)

Choristoderes are a group of Diapsids that might be Archosauromorphs, but their evolutionary relationships are somewhat uncertain. Choristoderes include animals like *Champsosaurus*, which, as you can see, resembles a small Crocodile, but differences in their skulls indicate that they are only distant relatives. Their long, narrow snouts with conical teeth are well-adapted for snaring Fish. *Champsosaurus* ribs were pachyostosic, which would have helped them achieve neutral buoyancy. They also had bones on their belly called **Gastralia**. You can see them really clearly on this specimen. They look like an extra set of ribs on the animal's stomach, which is why they are sometimes called **belly ribs**. They would have been useful for protection, achieving neutral buoyancy, and for making the body rigid. Choristoderes lived in the waterways of the Mesozoic along side the more famous marine Reptiles and were one of the rare clades of Reptiles that survived the End-Cretaceous mass extinction. Choristoderes finally went extinct about 20,000,000 y ago, during the Miocene-Epoch for reasons that are not entirely clear.

3.1.2.6 Tangasaurids

One clade of small Lizard-like basal Diapsids, the Tangasaurids, is known from the Permian of Madagascar.

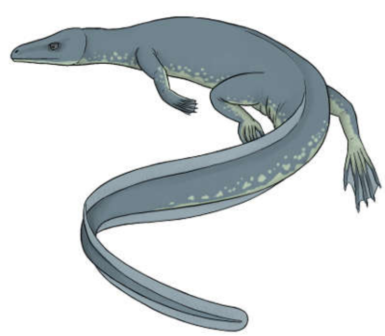


Illustration 33: *Hovasaurus* (Life restoration)

Based on this reconstruction, what aquatic problems was it adapted to solve?

A. Propulsion

B. Drag

C. Air breathing

D. Buoyancy

A few species within the Tangasaurids have long, flattened tails that would have been good for propulsion in the water, and the dense-boned *Hovasaurus* was found with **Gastroliths** preserved in the body, possibly used to achieve neutral buoyancy. We do not see a particularly streamlined shape compared to our terrestrial Reptiles, and the nares are not on the top of their heads. Therefore, **A** and **D** are the only correct answers. We are not exactly sure about all aspects of their ecology, but we think they were probably semi-aquatic.

Think back a couple of lessons when we discussed Thalattosuchians. It is interesting to note that they also developed adaptations for propulsion before they evolved adaptations for streamlining or surface breathing. As we introduce more transitional aquatic clades throughout this course, you should see that this pattern is pretty consistent.

Illustration 34: *Atopodentatus* (Life restoration)

Another unusual reptile of unknown relationships has one of the strangest skulls known from the Fossil record. It belongs to an animal called Atopodentatus. It had a downturned snout and lower jaw. The numerous teeth were very fine and needle-like, but the strangest thing is that the front of the snout was split up the middle, and also filled with these teeth. If you look at the Atopodentatus head on, it would have looked like a zipper was placed in the middle of its face. Atopodentatus was probably only semi-aquatic. It has the long body and short limbs characteristic of many swimming Reptiles, but the limbs appear to have been strong enough for terrestrial locomotion, and the hands and feet have small hooves, which are not known in any other marine reptile.

However, it probably did most of its feeding in the water, using the needle-like teeth as a sieve to filter out small prey from mud and sand. Where Atopodentatus fits on the tree of life is, again, contentious. It has a small pair of temporal characteristic of a Diapsid, but it was probably related to the Sauropterygians that we would study in lesson three.

3.1.2.7 Turtles

Surprisingly, one of the biggest phylogenetic problems within Amniotes is the placement of Turtles. Turtles have Anapsid skulls without temporal fenestra. This would normally indicate they are Parareptiles. However, many paleontologists have suggested that they are an early branch of Diapsids who have lost their temporal fenestra, converging on the Anapsid condition. Recent genetic analyses have hypothesized that they are closely related to the Crocodylomorpha.

For the purpose of this course, we are going to include them in their traditional position as parareptilian Amniotes. However, keep in mind that this debate is ongoing, and future discoveries may cause Turtles to be moved to a different part of the evolutionary tree. This is a good example of how the tree of life is always being revised as paleontologists find new specimens and reinterpret old discoveries in the light of new information.

What do we know about the evolutionary history of Turtles?

Illustration 35: *Odontochelys* (Life restoration)

The oldest Fossil Turtle, *Odontochelys*, is from the Triassic of China. *Odontochelys* is unusual compared to today's Turtles. It still possessed teeth and only had a partial shell protecting its belly. *Odontochelys* was found in marine sediments, and therefore, it appears that Turtles may have originated as aquatic Amniotes, and later lineages eventually returned to freshwater and terrestrial habitats.

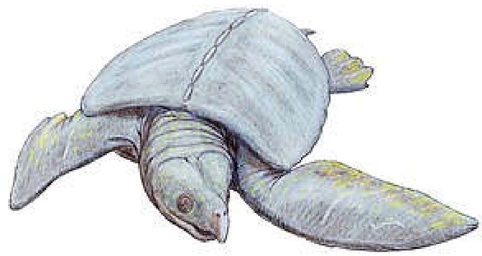


Illustration 36: *Archelon ischyros* (Life restoration)

In the Late-Cretaceous, an extinct lineage produced the largest marine Turtle that ever lived called *Archelon*, and it grew to lengths of >4 m.

3.1.3 Mesozoic Marine Ecosystem

At this point, I have introduced you to numerous clades of secondarily marine Reptiles that inhabited the World's Oceans before, and during, the Mesozoic. Including the three groups that will be the topic the following lessons. However, these Reptiles were far from the only animals in their habitats. They shared the seas with a huge diversity of other species, both vertebrates and invertebrates.

The Oceans of the Mesozoic were home to a wide variety of Fishes, including the ancestors of familiar modern Fish, like Salmon and Tuna, and some truly massive species that have no living descendants. Sharks were abundant too. They were frequent scavengers of the shallows. However, none of the large species of today had yet evolved. Reefs were built by Corals and Bivalves, including massive relatives of Oysters, like this one.

Illustration 37: Clam shell (Fossil)

3.1.3.1 Cephalopoda

A group of invertebrates that was much more abundant and diverse in the Mesozoic Oceans was the Cephalopoda. Today, Cephalopods are represented by Squid, Octopus, Cuttlefish, and the Nautilus. However, the Mesozoic seas were full of many other species that are now extinct, including Ammonites and Belemnites.

Illustration 38: Mesocoic Cephalopods (Life restoration)

Asteroceras (Ammonite) (left), Belemnoids (right)

Ammonites would have resembled a modern day Nautiluses in many ways. The soft, Squid-like part of their body would have resided within the coiled shell, which was composed of many chambers. Nautiluses can control gases within these chambers in order to regulate their buoyancy in the water, and spend their lives in the open Ocean feeding on small prey in the water column. Most Ammonites probably had a similar lifestyle, but their shells were often more elaborated than the smooth shell of the Nautilus, with a lot of bumps and ridges.

3.1.3.1.1 Belemnites

Belemnites more closely resembled Squid and Cuttlefish, and had an elongate internal shell, usually shaped like a fat pencil. Fossilized gut contents of several marine reptile specimens show that Cephalopods were a major part of the diet in many species.

3.2 Conclusion

In this lesson, we have discussed many amniote clades. Some might have been familiar to you already and some are probably new. In the next lesson, we will begin to look at Ichthyopterygians and their relatives.

Ichthyopterygians

1 Ichthyopterygian Systematics

1.1 Ichthyopterygian Relationships To Other Diapsids

Welcome back to marine Reptiles. In lesson two, we will examine the diversity of form and function for Ichthyopterygians and their closest relatives. The Ichthyopterygians are a distinctive and highly specialized group of marine Reptiles that lived from the Early-Triassic to the Mid-Cretaceous, over a span of nearly 150,000,000 y. They all had the same basic body plan, but were specialized in a variety of ways, ranging in length from 1 - 21 m. Some were small and snub-nosed, others had long pincer-like jaws, and still others had an overhanging upper jaw like a Swordfish. The derived members were streamlined like the fastest Fishes. They breathe through nostrils located between their eyes and propel themselves through the water using their crescent shape tail flukes.

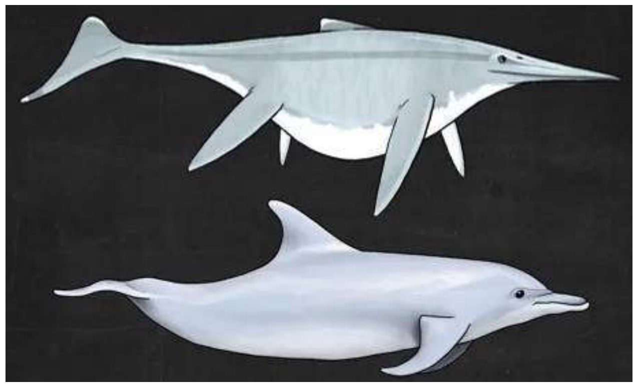


Illustration 39: Comparision between an Ichthyosaur (top) and a Dolphin (bottom)

They are an incredible example of convergent evolution, being similar in shape to Sharks, Tuna, and Dolphins. If a casual observer looked at a drawing of a Ichthyosaur and identified it as a Dolphin, this mistake could easily be forgiven. You can see that the two look very similar. However, a close examination will reveal some key morphological differences between them. If you compare these pictures, you might notice three major differences. On the Ichthyosaur, the breathing holes, or nares, are in front of the eyes instead of on top of the head. In addition, the tail fluke is vertical, like we would see on a Fish. It is not horizontal as we see on the Dolphin or any other marine Mammal. Finally, the Ichthyosaur had hind flippers that might of aided in steering. Even though these animals appear to be very similar, these key differences indicate that they evolved from different branches of the amniote tree.

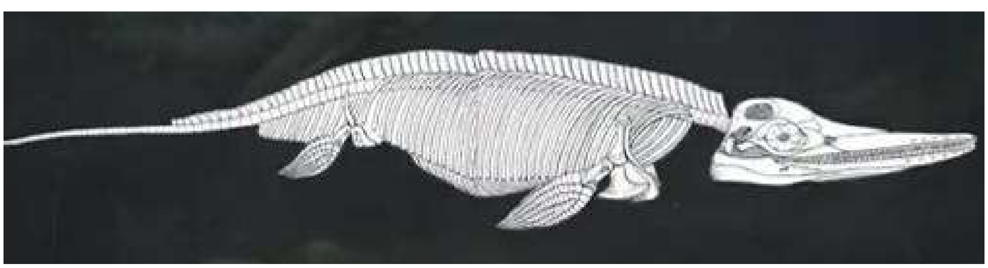


Illustration 40: Ichthyosaur (Generalized diagram)

Ichthyopterygians are best known for the Dolphin-like members of this clade, the Ichthyosaurs. Although Ichthyosaur means Fish-lizard, they were aquatic Amniotes, not Fish. Let us look at this generalized diagram of an Ichthyosaur, and see if we can figure out to which branch of the amniote tree these animals belong.

Ichthyopterygians had only one temporal fenestra, and so you might thing that they are Synapsid Amniotes, but Ichthyopterygians, and many other marine Reptiles we will discuss in this course, have a new kind of skull configuration called Euryapsid. Euryapsid skulls were once thought to represent a fourth branch of amniote diversity, but are now understood to be a modified Diapsid skull. Therefore, Ichthyopterygians evolved from ancestors with two openings in the skull behind each orbit. These openings are the upper and lower temporal fenestra. At some point, the bones behind the eyes got smaller and smaller, until eventually the lower temporal fenestra was lost, leaving only the upper temporal fenestra. The second temporal opening may no longer have been necessary after this group started swallowing their prey whole since temporal fenestra are associated with chewing muscles.

We can differentiate Synapsid and Euryapsid skulls based on which bones surround the fenestra. Even the earliest Ichthyopterygians show evidence of being well-adapted to a aquatic lifestyle. On land, the skeleton is essential for counteracting gravity, and a key element of the system is the tight articulation, or close connection, of the leg and hipbones to the spine. Aquatic organisms, supported by the water they live in, do not need a pelvic girdle capable of supporting their bodies. Even primitive Ichthyopterygians have lost the boney connection between their pelvic girdle and their spines. Like Whales today, the pelvic girdle floated in the layers of muscle of the abdominal wall. You can see this quite clearly in this skeleton.

As is typical of many marine Reptiles that evolved during the Triassic Period, the exact evolutionary relationships of Ichthyopterygians are still unresolved. They appear very suddenly in the Fossil record, and the oldest examples are fully adapted aquatic forms. We have not yet discovered any transitional forms. Therefore, we really do not know exactly how they evolved or from what.

There are three major hypotheses about which Sauropsid group Ichthyopterygians are belonging. Ichthyosaurs might be basal Diapsids, Lepidosauromorphs or even Archosauromorphs. In this course, we will use the most conservative hypothesis and place Ichthyopterygians as a separate branch of Diapsida. Let us look at some of the members of the group.

Since Ichthyopterygians appeared suddenly in the Fossil record, and no transitional forms have been found, it is difficult to know to what other Reptiles they are most closely related. Two possible candidates are the Thalattosaurs and the Hupehsuchians.

1.1.1.1 Thalattosaurs

Illustration 41: *Thalattosaur* (Fossil)

Thalattosaurs are large Triassic marine Reptiles with paddle-like feet and long snouts. They are an interesting clade of Triassic marine Reptiles that are sometimes considered basal Diapsids, but recent research suggests that they are close relatives of Ichthyopterygians. Overall, Thalattosaurs looked a lot like large aquatic Lizards. The joint surfaces on their limb and pectoral and pelvic girdles indicate that they were not suited for extensive terrestrial locomotion. Some of the more derived Thalattosaurs had paddle-like hand and feet, but they never evolved flippers. All Thalattosaurs had long snouts and retracted nares that were close to the orbits.

1.1.1.2 Hupehsuchians

Illustration 42: *Hupehsuchus (*Fossil)

Another small and enigmatic clade of possible Ichthyopterygian relatives is the Hupehsuchia, which are known exclusively from the Triassic of China. Hupehsuchians have fusiform bodies similar to Ichthyosaurs. However, Hupehsuchians also have some unique features. They have long, pointed snouts, but lack teeth entirely. Their limbs are paddle-shaped rather than true flippers, and there is a unique pattern of Osteoderms, or plate-like bony deposits in the skin, along the tops of the vertebral column. They also have Gastralia, or belly ribs. Together with the Osteoderms, these would have increased the density of Hupehsuchians bodies. Their increased density would have helped Hupehsuchians achieve neutral buoyancy.

Morphological similarities suggest that Hupehsuchians and Ichthyopterygians are closely related. However, there are differences that indicate Hupehsuchians might have evolved Ichthyosaur-like features convergently. This could mean that they are a different lineage of the Diapsid family tree.

1.1.2 Ichthyopterygian Diagnostic Characters

Like all clades, Ichthyopterygians are grouped together, because they share a certain set of features. Such features or sets of features, which are unique to a group and differentiate them from other lineages are known as **diagnostic characters**. Because Ichthyopterygians are long extinct, the features scientists use to define this group all come the one source of information available to them: preserved skeletal remains.

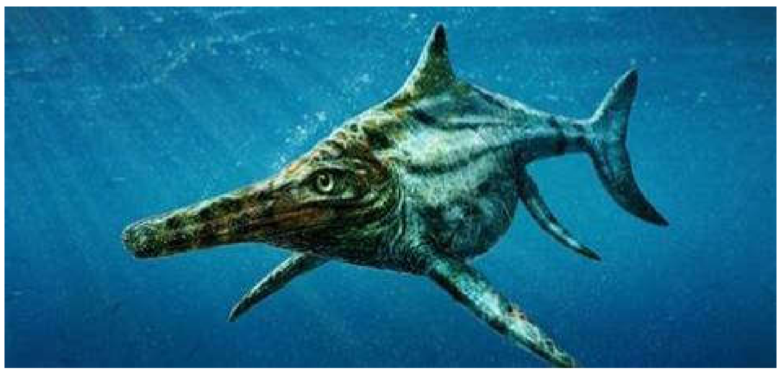


Illustration 43: Ichthyosaur (Life restoration)

Now that we have looked at some possible relatives of the Ichthyopterygians, let us take a closer look at Ichthyoperygia proper. The most famous members of the Ichthyopterygia are the Ichthyosaurs, and the most derived Ichthyosaurs have fusiform bodies with a crescent shaped vertical tail fluke. Their vertebrae have morphology that we call **amphicoelous**, which means that both faces of the disk are concave.

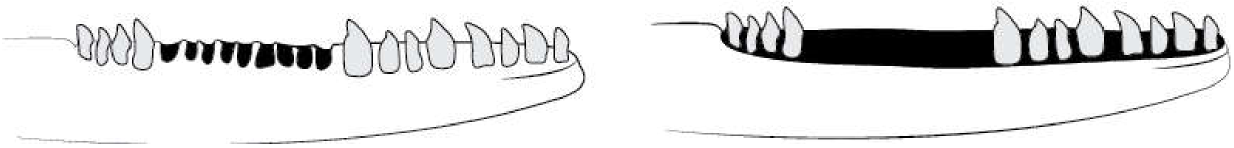


Illustration 44: Teeth grown in individual sockets (left) and teeth grown from a single groove (right)

In the skull, Ichthyosaurs typically have a long snout and the teeth are set in a groove rather than in sockets like most marine Reptiles. They also have a large orbit and a reduced cheek region.

Illustration 45: Ichthyosaur tooth (Fossil)

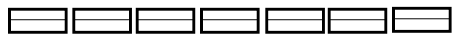
Ichthyosaur teeth are distinctive, because in most species the base of the tooth has a fluted, grooved external appearance. This easily recognizable external texture reflects an internal pattern of folding in the dentine of the tooth, known as **plicidentine**.

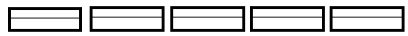
1.1.3 Vertebrae And Motion

The spinal column provides necessary support to an animal. It needs to provide more support on land and less in the water, but the spine also limits the flexibility and type of motion that an animal can perform. Think of the vertebral column is a string of beads.

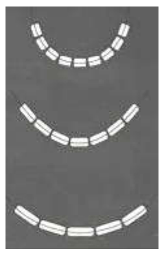
Which of these beads strings would be the most flexible?

A. 

B. 

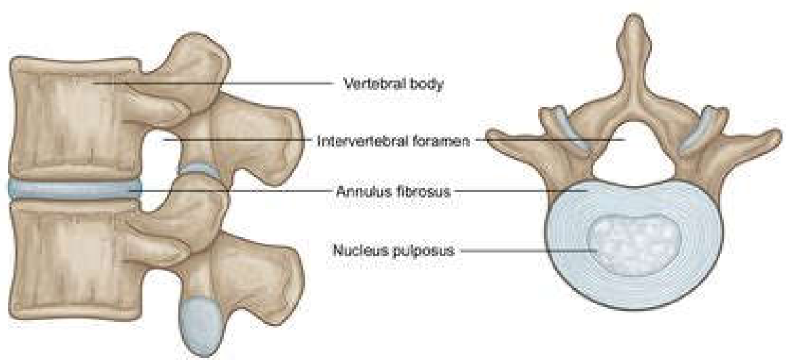
C. 

Think about a string of beads. If the beads are shaped like long narrow cylinders, like many vertebrae are, the string can only flex in-between each bead. Decreasing the length between each bead increases flexibility, because there is less distance between each joint.



Therefore, the shortest vertebrae make the most flexible spinal column, and the long vertical cylindrical vertebrae would result in the least flexible spine. That makes **A** the correct answer.

Ichthyopterygians have more vertebrae in their torsos and tails than most terrestrial Reptiles do. They have more than 40 vertebrae between their head and pelvic girdle and up to 80 vertebrae in their tails. The increased number of vertebrae facilitated the axial undulations necessary for anguilliform swimming. Early-Ichthyopterygians had vertebrae that were longer than they were wide, kind of like this Mosasaur vertebra.



Throughout their evolutionary history, the vertebrae developed into the characteristic concave disk shape, like this.

Illustration 46: Bison vertebrae

In terrestrial vertebrates, the vertebrae have complex neural spines. These blade-like **processes** come off of the vertebrae, as you can see on this bison vertebra, and processes on the **neural spines** allow tight articulation to help support the body against gravity. Ichthyopterygian neural spines are less complex, poorly attached, and this increases the flexibility of the spinal column.

1.1.4 Ichthyopterygian Phylogeny

1.1.4.1 Ichthyopterygia

The Ichthyopterygian lineage spanned 150,000,000 y. Ichthyopterygians first appear in the Fossil record during the early parts of the Triassic-Period. The earliest Ichthyopterygian is a small 1 m long animal called *Parvinatator*, which remains poorly known to this day. However, paleontologists do know that this taxon displayed the beginnings of a trend that more derived Ichthyosaurs would take to an extreme: hyperphalangy. If you look at your own hand or foot, you will see that you have two or three segments to each finger or toe, which are known as digits. Each of these segments is an individual bone called a phalanx. Many terrestrial Tetrapods also have two or three phalanges in their digits. However, it is common for aquatic Tetrapods to develop many extra phalanges as their terrestrial limb lengthens into a fin. Parvinatator was already well-adapted to its aquatic environment, and had up to five phalanges in each digit. Some of the more derived Ichthyosaurs we will learn about later had as many as 30 phalanges per digit.

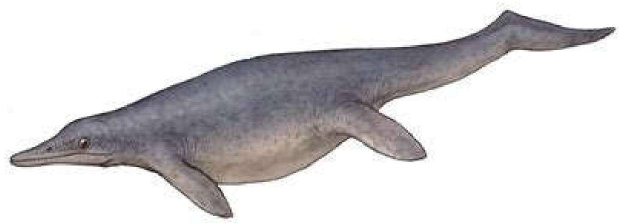


Illustration 47: *Utatsusaurus* (Life restoration)

Illustration 48: *Grippa longirostris* (Life restoration)

Other early Triassic Ichthyopterygians include the fully aquatic *Utatsusaurus* and *Grippia*. The teeth of *Utatsusaurus* were still set in shallow sockets, but the dental groves seen in more derived Ichthyosaurs had also started to form. *Utatsusaurus* also has a long, narrow humerus, which is typical for terrestrial Tetrapods, and at the more aquatic *Grippia*, the humerus is wider then it is long. Unlike more derived Ichthyosaurs, *Utatsusaurus* and *Grippia* lacked dorsal fins, probably did not have prominent tail flukes, and had longer, more sinuous bodies, because they had more vertebrae in their spinal column. These traits tend to be representative of anguilliform swimmers.

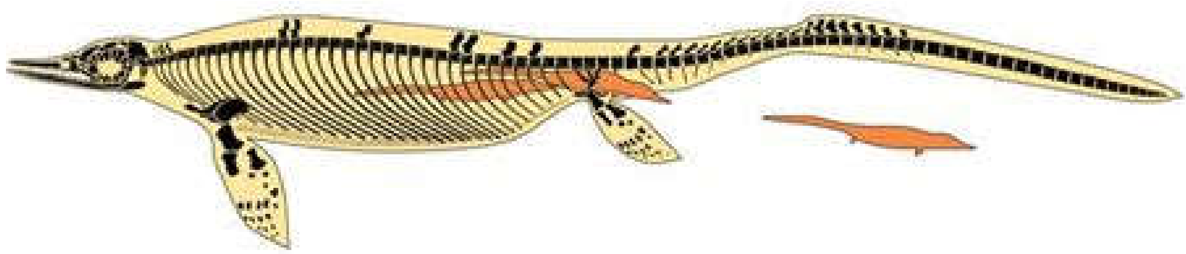


Illustration 49: Chaohusaurus (Giving live birth, life restoration)

Related to *Grippia* is a genus from the Early-Triassic of China, *Chaohusaurus*. This small Ichthyopterygian never grew longer than 2 m. Chaohusaurus also had multiple rows of crushing teeth in its upper jaw. Its limbs had developed into primitive flippers, but the pattern of bones in the fingers more closely resembled terrestrial Tetrapods. Despite its primitive number of phalanges, Chaohusaurus is believed to have been fully aquatic, as the limbs are well-developed flippers. New fossils of Chaohusaurus include pregnant females, which show three embryos in the mother's abdomen. This demonstrates that these primitive Ichthyopterygian gave live birth in the water.

Another possible basal Ichthyopterygian is *Omphalosaurus*. This animal is definitively fully aquatic and shares many features in common with basal Ichthyopterygians, like *Utatsusaurus* and *Grippia*, but its teeth look very different from other Ichthyopterygians. Instead of rows of conical Fish-eating teeth, *Omphalosaurus* has a pavement of rounded, bulbous teeth across most of the front of its lower jaw. We would normally expect to see teeth like that in the durophagous animal, one that uses powerful crushing bites to break down hard prey, but the skull of *Omphalosaurus* was not suited to biting down hard. Having crushing teeth far away form the jaw joint means that the jaw is not optimized for powerful bites. It is unclear exactly what it would have eaten. Even though the external shape of the teeth is different from most Ichthyosaurs, the presence of plicidentine inside the teeth suggests that it is probably an Ichthyopterygian.

1.1.4.2 Ichthyosauria

Imagine a basal Ichthyosaur that was 10 m long with an incredible 60 vertebrae in front of the pelvis. Now imagine it also had a tail without a fluke, and no dorsal fin. Finally, imagine that it had very small eyes and a long snout full of robust, conical teeth.

Which of the three descriptions below do you think would best describe this Ichthyosaur? Remember, we covered anguilliform, carangiform, and thunniform swimming in lesson one.

A. An anguilliform swimmer that grazed in shallow water

B. A carangiform swimmer that hunted in deep water

C. A thunniform swimmer that hunted in shallow waters

Illustration 50: *Cymbospondylus youngorum* (Life restoration)

The Ichthyosaur we just described is called *Cymbospondylus*. Its large, conical teeth meant that it was a hunter, which probably preyed on Fish and Cephalopods. The lack of a tail fluke indicates that it was probably not a thunniform swimmer. Therefore, the correct answer here is **B**. It probably hunted in deep water where there was abundant Fish and Cephalopods, and it was most likely a carangiform swimmer.

Now, let us go on to discuss this genus and others like it. The most derived Ichthyopterygians formed the clade Ichthyosauria. They are united by the presence of nares that face laterally rather than being on top of the skull. Some of the earliest true Ichthyosaurs were genera like *Cymbospondylus* and *Mixosaurus*. *Cymbospondylus* was the first large Ichthyosaur growing to 10 m long, about the size of an adult male Orca. This Ichthyosaur was very elongate. It had 60 vertebrae in front of its pelvis and its very long tail would have assisted in propulsion. *Cymbospondylus* also had a much longer snout then earlier Ichthyopterygians. It also has the smallest orbit, and therefore, the smallest eye of any known Ichthyosaur.

Mixosaurus represents further steps towards solving the aquatic problem. Instead of a Lizard-like body with a paddle-like tail, it had a more fusiform, streamlined body, a small dorsal fin for stability, and a lower tail fluke for added propulsion. The amphicoelous shape of the vertebrae gave greater flexibility to the spine and probably resulted in an anguilliform swimming style similar to more primitive Ichthyopterygians.

The biggest Ichthyosaur of them all has been found in British Columbia and is named *Shonisaurus*. It was at least 21 m long, which is about the size of a finned Whale. The skull alone would have been over 3 m, but paleontologists think they likely did have a low tail fluke to generate additional thrust. The vertebrae in this group had developed into the disc-like morphology characteristic of the derived Ichthyosaurs. They also lacked teeth as adults, and so what they ate is a mystery. Some paleontologists think they may have swallowed soft-bodied Cephalopods whole.

Shastasaurids and their early relatives, though not as derived as later Ichthyosaurs, had already evolved to solve many of the issues associated with the aquatic problem.

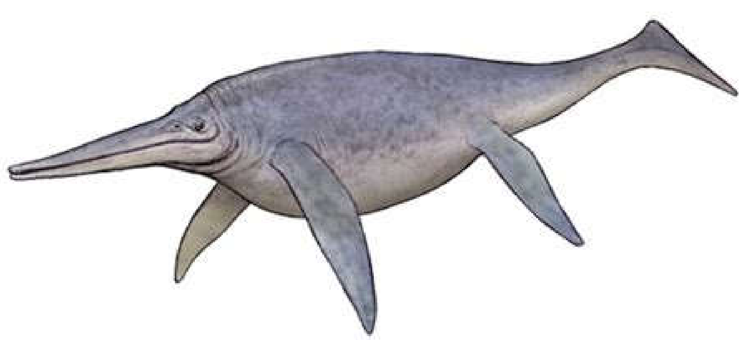


Illustration 51: Shastasaurid (Life reconstruction)

Based on this reconstruction of a Shastasaurid, select which aspect of the aquatic problem these Ichthyopterygians had probably solved.

A. Drag
B. Stability
C. Propulsion
D. All of the above

Early Ichthyosaurs were already extremely well-adapted to their aquatic environment. Their bodies were streamlined to counteract drag. They had dorsal fins for stability in a 3D environment. They had laterally compressed tails to generate propulsion, and their nares had migrated to the top of their heads to facilitate breathing at the surface. Therefore, the correct answer is **D**.

1.1.4.3 Euichthyosauria

Ichthyosaur is more derived than the Shastasaurids form the clade Euichthyosauria, and are united by the loss of the bony attachment between teeth and jaws. The majority of Euichthyosaurians are in the clade Parvipelvia. Ichthyosaurs of this clade are united by straight as opposed to plate-like scapula, a radius wider than it is long, and a reduced, narrow pubis. A unique family within this clade is Leptopterygiidae. They have converged on a similar morphology with Swordfish, having a very narrow elongate upper jaw, sometimes greatly overhanging the shorter lower jaw.

1.1.4.4 Parvipelvia

One species was named *Excalibosaurus*, both for its sword-like jaw and for the fact that it was found in England near where King Arthur's legendary sword was supposed to have emerged. In another species, *Eurhinosaurus*, the upper jaw bears teeth even beyond the contact with the lower jaw. We are not certain what these strange animals ate, but they probably had similar feeding habits to Swordfish that use their extended rostrum, or snout, to slash at and injure prey making it easier to catch and swallow.

The genus Temnodontosaurus contains many species, including some of the first Ichthyosaur fossils ever discovered. Unlike most Ichthyosaurs within Parvipelvia, species of Temnodontosaurus had fewer than five digits in their flippers. The phalanges in the first digit were notched, possibly for the attachment of the soft tissues that covered their limbs.

1.1.4.5 Thunnosauria

The final Ichthyosaur group we will discuss is the Thunnosauria.

Illustration 52: Thunnosauria (Fossil)

Paleontologists consider this clade to be the best adapted to the marine environment. Look at this reconstruction. Why do paleontologists think this?

A. They eat only fast moving prey such as Tuna
B. Like Tuna, they evolved gills so they could stay underwater indefinitely
C. When they were first discovered, early paleontologists mistook them for Tuna
D. Their body plan resembles a Tuna, which are some of the strongest swimmers alive today

Since Ichthyosaurs are Reptiles, they have different skeletons than Fish, and they never evolve gills, therefore, B and C are incorrect. Thunnosaurs certainly ate fast moving prey, but like any predator, they would have eaten anything they could, including slow prey. Therefore, A is incorrect. The correct answer is **D**. Tuna are some of the strongest swimmers in today's Oceans.

Thunnosaurs looked very similar to Tuna, and therefore, were probably the fastest, best adapted of all the Ichthyosaurs. As noted in the previous question, the most highly derived clade is the Thunnosauria, named for their resemblance to the strongest open Ocean cruisers of today: Tuna.

The species in this clade are united by fore flippers twice as long as their hind flippers. These Ichthyosaurs also have much more exaggerated down turn bends to their tails. The tail bend is formed by a few wedge shaped vertebrae, and the vertebrae behind this kink would have supported the bottom half of a crescent shaped tail fluke.

The most basal Thunnosaur is *Ichthyosaurus* found near Lyme Regis on the South coast of England in the early 1800's. These Ichthyosaurs had flippers, well-adapted to an aquatic life. They had advanced hyperphalangy, and a condition called hyperdactyly. Not only did they have at least 25 bones in an individual digit, but also they could have nine or more digits in each flipper. These adaptations would have made the flippers larger, stiffer and solid for stronger, faster, and more precise changes of direction. The genus *Stenopterygius* and even more derived Ichthyosaurs are characterized by fusion of the Pubis and Ischium into a single pelvic element. *Stenopterygius* is known from thousands of beautifully preserved fossils, including numerous pregnant females.

Illustration 53: *Ophthalmosaurus*

Ophthalmosaurus is another Thunnosaurid, well-known from around the World. It had the largest eyes, relative to its skull, of any vertebrates that has every lived. Its eyes were the same size as those of a blue Whale, an animal almost seven times larger.

The most derived genus of Ichthyosaur, one of only a few that survived into the Cretaceous, is *Platyperygius.* There are several species within this genus, but they all exhibit extreme hypertadactyly and hyperflangy, with at least seven digits containing up to 30 short blocky phalanges in their fore flippers.

In this first section, I presented you with a sample of Ichthyopterygian diversity. Before we go one to discuss some of the ways Ichthyosaurs solved the aquatic problem, take a moment to review the species.

2 Ichthyosaur Paleobiology

Now that we have examined some of the diversity of Ichthyosaurs let us now investigate their paleobiology. Just like the Mammals that evolved into Whales and Dolphins, the Reptiles that returned to the sea and acquired characteristics that made life in the water possible. They evolved the fish-like shape, flippers instead of feet, a mouth full of sharp teeth for capturing slippery prey, and the ability to give birth in the water. Like Mammals, Ichthyosaurs were air breathers; this restricted the amount of time they could spend underwater.

Ichthyosaurs occupied both coastal environments and open Oceans. Fossilized remains in their stomachs tell us that they ate mostly Cephalopods and Fish, but also supplemented their diets with Turtles, smaller Ichthyosaurs, and the drowned carcasses of other animals. They had large eyes capable of seeing in deep, murky water and likely hunted primarily using their sense of sight.

In the next section, we will explore how the fossils of Ichthyosaurs have informed paleontologists about their possible **paleoecology**: feeding, locomotion, and reproduction.

2.1 Feeding

One of the most important aspects of the biology of an animal is what and how it eats. Because water is so dense, aquatic animals face unique challenges in simply getting food close to their mouths, let alone inside.

What do you think happens to a Fish when an Ichthyosaur tries to close its mouth to catch it?

A. The Fish is sucked inside the Ichthyosaur's mouth

B. The Fish remains stationary relative to the Ichthyosaur's mouth

C. The Fish is pushed out of the Ichthyosaur's mouth

An animal swimming through the water will always push some water ahead of it, which means, the water pushes the prey away from it. The same thing happens when it starts to bite down on its prey. The water displaced by the closing jaws, shoots away from the mouth, taking the prey with it. Therefore, the correct answer here is **C**.

How did Ichthyosaurus catch their prey?

2.1.1 Ram Feeding

One feeding strategy is called ram feeding. Ram feeders, like Whale sharks, let the water flow into their mouths and right back out through their gills. The food is strained out of the water by special structures called gill rakers.

2.1.2 Lunge Feeding

Illustration 54: Baleen in a Whales mouth

Humpback and Blue whales use a special kind of ram feeding called lunge feeding. They accelerate through the water towards their prey, and then open their mouth extremely wide. They have special folds in their throat that allows the skin to expand rapidly outward like a parachute. They then push the water back out of their mouth through baleen, which is a fibrous material that has replaced their teeth. Since ram feeders often filter their food out of the water, we can also call them **filter feeders**. It is possible that some of the large, toothless Ichthyosaurs may have used this feeding strategy, but we have never found fossils of any specialized mouthparts that prove it.

2.1.3 Manipulation (Or Biting)

Most Ichthyosaurs used manipulation or biting to capture their prey. This can be used for acquiring prey that lives on the bottom of the sea floor, like Shellfish, which would not be pushed away by water as a predator approaches. It is also used for snatching up small prey in the open water and for biting pieces off of larger prey.

2.1.4 Teeth

We can use details of the teeth, like the shape, size, or wear patterns, to understand what kinds of prey Ichthyosaurs ate, and how it was caught. Using those features, we can group Ichthyosaurs into **feeding guilds**. Guilds are groups of species, which are not necessarily closely related, but that use similar resources in their environment.

Some of the guilds that have been identified for marine Reptiles are the **Crush, Smash, Pierce**, and **Cut Guilds**. Look at the tooth shape seen in each of these guilds. Tooth shapes can be matched to the type of prey for they were best adapted.

2.1.4.1 Crush Guild

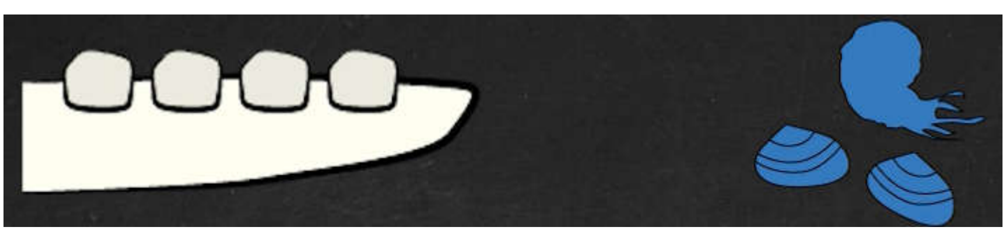


Illustration 55: Crush guild member teeth (left) and example prey (right)

Crush guild members had robust crushing teeth for eating hard preys, therefore, they most likely ate Mollusks and Ammonites. Marine Reptiles in the smash guild had small teeth with rounded points, crushing and smashing might sound similar, but crushing was used for hard prey items and smashing was used for softer prey, like Squid.

2.1.4.2 Smash Guild

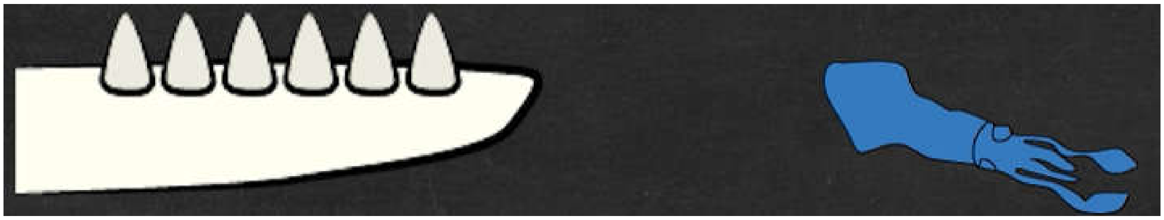


Illustration 56:Smash guild member teeth (left) and prey (right).

Long pointed teeth for trapping and piercing soft prey were characteristic of the pierce guild, therefore, they ate small Fish.

2.1.4.3 Pierce Guild

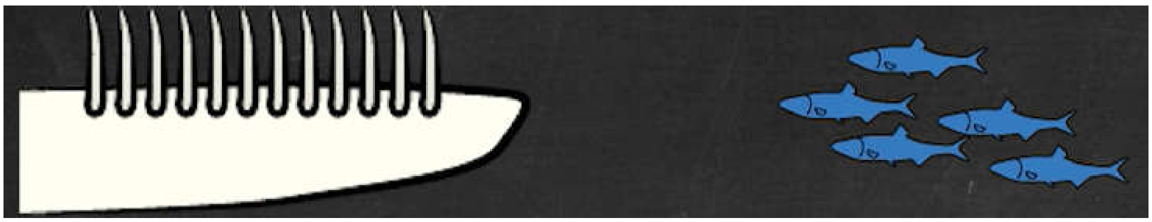


Illustration 57: Pierce guild member teeth (left) and prey (right)

Pointed teeth with cutting edges perfect for tearing off chunks of large prey were characteristic of the cut guild, which specialized in eating very large prey. Species in the cut guild were usually the Apex Predators in their ecosystem, meaning they were at the top of the food chain.

2.1.4.4 Cut Guild

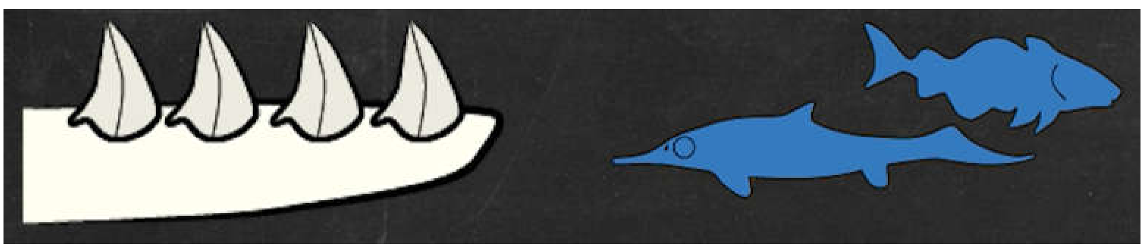


Illustration 58: Cut guild member teeth (left) and example prey (right)

We find independent support for these guilds by looking at preserved stomach contents. Most Ichthyosaurs occupied the smash and pierce gills and fed on soft-bodied Fish and Cephalopods. We know this because Ichthyosaurs' stomach contents have Fish bones and hooks from the suckers of Squid. Most scientists agree that they probably swam through schools of Fish or Squid and snapped up the smaller animals, similar to the way Dolphins hunt today. It is likely they detected prey using extremely acute vision and a strong sense of smell, as indicated by their enormous eyes and olfactory channels. They probably could not hear very well, having uninsulated middle ears, and thick, non-sensitive inner ear bones.

2.2 Locomotion

Most derived Ichthyosaurs actively chased down prey and used manipulation to get their prey into their mouths. Let us talk about some of the evolutionary adaptations enable the Ichthyosaurs to be such successful pursuit predators.

Illustration 59: *Chaohusaurus brevifemoralis* (Fossil)

The most basal Ichthyopterygians with long, serpentine bodies like *Utatsusaurus* and *Chaohusaurus* would not have been efficient, high-speed, long distance pursuit predators. However, their long bodies and tails were well suited for short bursts of rapid acceleration and quick turning; therefore, they probably ambushed their prey instead.

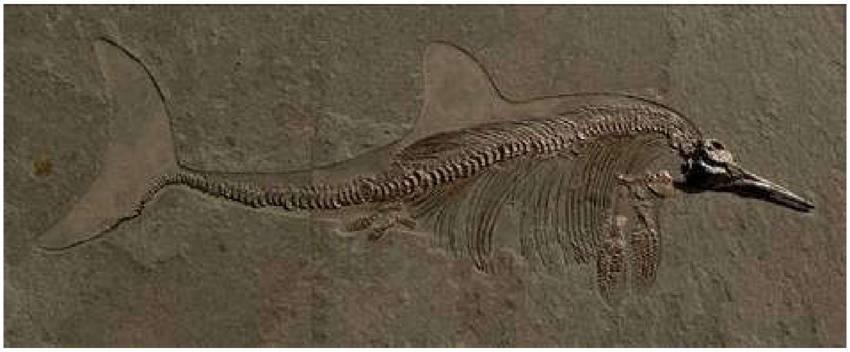


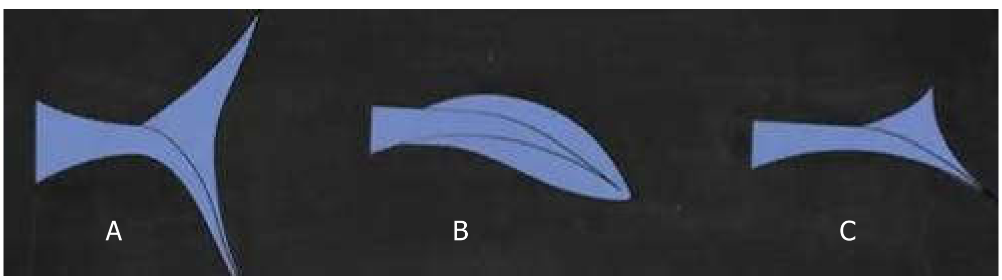
Illustration 60: *Stenopterygius quadriscissus* (Fossil)

More derived Ichthyosaur, like *Stenopterygius*, evolved streamline tuna-like body shapes with a shorter torso and a tall, efficient crescent shaped tail fluke. Similar body shapes we find today in fast-swimming Sharks, Dolphins, and Fish, like the Mako Shark, the Spinner Dolphin, and the Tuna. This body shape allows for high-speed cruising with minimal energy expenditure, which is an important quality for pursuit predators.

2.2.1 Ichthyosaur Tails

Ichthyosaur tails went through multiple stages before evolving the convergent, highly efficient, crescent shape fluke. In basal Ichthyosaurs, like *Grippia*, the tail stretched straight out behind them, and was laterally flattened.

Below are several Ichthyopterygian tails.



Which one is the most derived?

A. The crescent-shaped tail of *Platytergius*

B. The laterally flattened tail of *Grippia*

C. The low tailfin of *Mixosaurus*

In basal Ichthyosaurs, the tail stretched straight out behind them and was laterally flattened like tail B. Throughout their evolution Ichthyosaurs began to develop a downward tail bend to support the longer bottom lobe of a tail fluke, and a cartilaginous blade to support the shorter top lobe like tail C. Over time the bend got sharper and the lobes of the tail fluke got longer and more equal in size like tail A. The shape of tail C, where one lobe is longer than the other is known as heterocercal. The heterocercal shape helps the animal change directions and accelerates when swimming. As time when on, the crescent-shaped tails of more derived Jurassic and Cretaceous Ichthyosaurs became increasingly symmetrical, a shape we call homocercal. **A** is the most derived tail form of the three and thus the correct answer.

2.2.2 Ichthyosaur Bodies

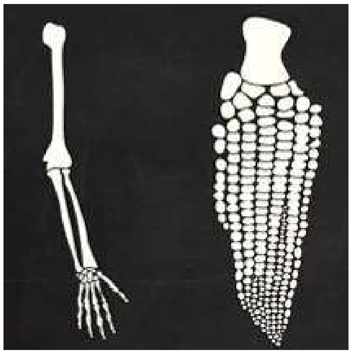
In addition to evolving this crescent shaped, homocercal tail, Ichthyosaurs also required other changes to their morphology before they converged on the highly specialized Tuna-like body plan. Support for the tail driven swimming also required the vertebrae to change, as we discussed earlier.

The vertebrae of basal Ichthyosaurs were long and narrow, conducive to flexible oscillatory swimming. As time went by, they became shorter, flatter, and less flexible, allowing the Ichthyosaurs to evolve towards thunniform swimming. In order to achieve maximum speed, more is required than a strong propulsive tail to generate thrust. A moving object encounters a lot of inertial viscous drag as it moves through the water. Therefore, maximum speed and efficiency in the water requires a smooth, streamlined shape.

As discussed, Ichthyosaurs converged on a fusiform body shape that allowed them to cut through the water easily, similar to torpedos and submarines. It is possible that some of the most derived Ichthyosaurs even lost their scales and were covered in smooth skin that reduced viscous drag. A tall dorsal fin made from a blade of cartilage provided stability when moving through the water at high speeds. Minimizing drag and generating thrust was not the end of the locomotive problems facing Ichthyosaurs, they also had to steer, which would have been primarily accomplished by the flippers.

2.2.3 Ichthyosaur Flippers

Ichthyosaurs are amniote Tetrapods. Therefore, we share many of the same bones in our own skeleton. However, Ichthyosaur hands and feet are different.



Compared to a human skeleton, which differences do you notice? Choose all that apply.

The Ichthyosaur hand has:

A. More finger bones

B. More fingers

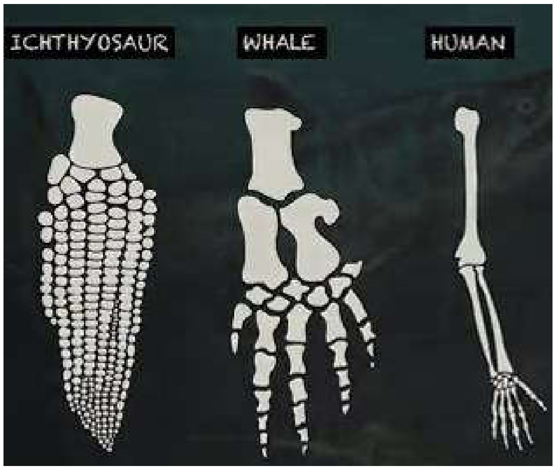
C. No humorous

D. Large claws

Ichthyosaurs have four flippers that contain the same arm and leg bones as you and I have. Therefore, they still have a humerus, which makes C incorrect. Additionally, like you and I, Ichthyosaurs did not use their limbs as weapons; therefore, it was more important for their limbs to become streamlined than to retain unnecessary claws, so D is incorrect.

However, as you can see, Ichthyosaurs have many, many more bones in each finger. Instead of having the two finger bones, called phalanges in our thumb, or three phalanges in our other digits, a single Ichthyosaur digit might have 20 phalanges or more. Some Ichthyosaurs even branch some of their fingers into additional digits. We call the addition of more finger bones, hyperphalangy, and the addition of new digits, hyperdactyly. Therefore, the correct answers are **A** and **B**.

In the evolution of Ichthyosaurs flippers, we can see a different solution to the problem of steering in water. As you just saw, Ichthyosaur flippers are very different from a terrestrial limb. The flippers of Whales, Seals, and Manatees all have five internal fingers, demonstrating that these marine Mammals are descended from terrestrial Tetrapod ancestors. It is a bit of a surprise then to see the derived Ichthyosaur solve the problem of flipper design in a completely different way.



As with marine Mammals, we see a reduction in the length of the arm bones, including the humerus, ulna, and radius, but instead of seeing separate fingers as in marine Mammals, derived Ichthyosaurs have a mass of tile-shaped bones packed together; therefore, that they form a solid flipper shaped mosaic. In the most derived Ichthyosaurs, the number of digits varied from three to nine, and the hyperphalangy became extreme, with as many as 30 phalanges in a single digit, as in *Platypterygius*.

2.2.4 Diving Behavior

Paleontologists think that some derived Ichthyosaurs were not just strong, efficient swimmers, but also accomplished divers. Yet, most Ichthyosaur fossils that we find are preserved in coastal environments.

How did paleontologists conclude that some of these animals spent time diving? Check all the answers you think apply.

A. They have big eyes to see in the dark

B. They have large tails to drive them down

C. They got the bends, like scuba divers

D. They had extra heavy bones to help them sink

Plenty of animals that live only at the surface of the water have large tails, and many animals that dive have smaller tails than relatives that live on the surface; therefore, B is not correct.

Diving animals also do not tend to have heavier bones, since being neutrally buoyant is more efficient; therefore, D is not correct.

Ichthyosaurs had some of the biggest eyes of any vertebrates, which probably would have helped them to see in deep, dark water; therefore, **A** is correct.

Ichthyosaurs also show evidence of a bone disease called the bends, which affects scuba divers today; therefore, **C** is also correct.

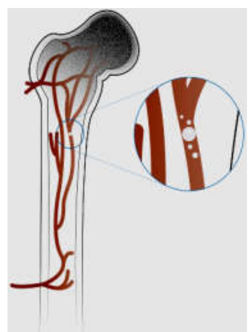
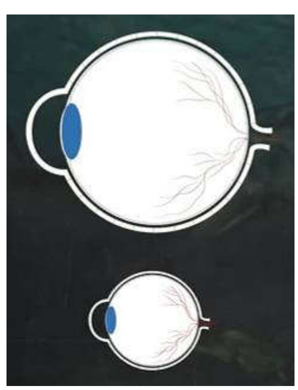


Illustration 61: Bubbles present in the blood (the bend)

Let us go into some more detail about these adaptations to deep diving. The high pressure experienced in deeper waters poses a unique set of problems to an air breathing tetrapod. The gases absorbed into the bloodstream are carried throughout the tissues of the body. During a dive, if the animal ascends too quickly, the sudden drop in pressure can cause the dissolved gases to come out of the blood and form tiny bubbles. This leads to the condition called the bends, and some fossils provide evidence that Ichthyosaurs also got these bends.

If a bubble in a bone cuts off blood supply, the surrounding bony tissue dies from a condition known as avascular necroses. Avascular necrosis causes the dead region of the bone to collapse. Therefore, unusual depressions on the surface of bones, or collapsed, dense regions seen in X-rays, allow paleontologists to recognize cases of avascular necrosis.



We have mentioned a few times, how large Ichthyosaur eyes could be. This exaggerated feature provides paleontologists, with additional support, for the diving habits of Ichthyosaurs. The cells that line the back of the eyeball and collect light are called photoreceptors. More photoreceptors allows for greater light collection and better vision in the dark. A larger eyeball can have more photoreceptors, and therefore, greater low light vision.

Illustration 62: *Temnodontosaurus* (Life restoration)

Temnodontosaurus, with it is 25 cm in diameter eye, would have had enough photoreceptors to absorb what little light potentially penetrates to a water depth of 150 m!

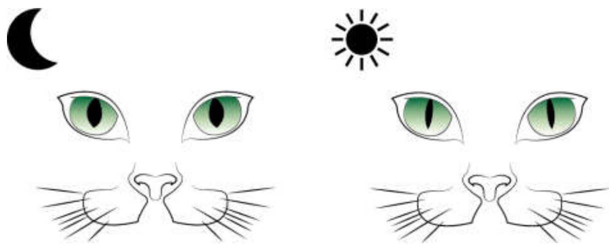


Illustration 63: Aperture of Cat eye at night (left) and during the day (right)

The maximum aperture, or diameter of the opening, that let us light into an eye, also determines how well an animal can see in the dark. For example, cat eyes have very large apertures. If they could swim and dive, cats would be able to see and hunt Fish 500 m below the surface. *Ophthalmosaurus* had the largest aperture of any Ichthyosaur. The proportions of the aperture to the eye were similar to that of a cat. These estimations suggest that Ichthyosaurs could have hunted by sight in deep, dark water.

Some studies have compared the occurrence of avascular necrosis and the diameter of Ichthyosaur eyes, and it does appear that Ichthyosaurs with large eyes were more likely to have experienced decompression sickness, which solidifies the evidence that large-eyed Ichthyosaurs, like *Ophthalmosaurus*, performed deep dives regularly.

2.2.5 Cold Water = Cold Reptile?

Unfortunately, the fact that Ichthyosaurs were pursuit predators who dove to hunt raises yet another problem. The Ocean, especially the deep Ocean, is very cold. As discussed in a former lesson, water is an extremely good heat conductor, sapping body heat very quickly. When the body temperature of a Reptile drops too low, they become sluggish, inactive and not very good hunters.

How could Ichthyosaurs possibly have lived in the Heat-sapping Ocean all their lives, without being slow and sluggish? Check all that could apply.

A. They only lived in warm places

B. They produced their own body heat

C. They basked in the sun to warm up

D. They had to stay active to keep themselves warm

The Ichthyosaur's active aquatic lifestyle itself may have helped them stay warm. Terrestrial Reptiles use about 75 % of their locomotion energy simply to support their own weight. Since water supports the bodies of aquatic Reptiles, all their locomotion energy is available for propulsion. This greater efficiency allows them to fuel high energy, heat-generating activities such as hunting, for much longer. Therefore, **D** is correct.

Ichthyosaurs lived worldwide, including in colder Arctic waters; therefore, A is incorrect. It is also unlikely that they would have basked in the sun very often, as this would have left them vulnerable to predators; therefore, C is incorrect.

Finally, **B** may also be correct, since it is possible that Ichthyosaurs actually generated their own internal body heat. We will now discuss this in more detail.

2.2.5.1 Endothermy

Like all animals, Ichthyosaurs would have been slow and sluggish when they were too cold. We know that Ichthyosaurs were able to move quickly, because they were highly derived pursuit predators, capable of catching fast moving prey, like Fish. Since water is such a good heat conductor, Ichthyosaurs must have had adaptations to maintain their internal temperature. They may have done this by actually generating their own body heat, a process known as endothermy.

Many modern Fish, such as Tuna and the great White Shark, do this by partially heating their muscles using a special kind of circulatory system. Their high metabolism allows them to heat up a small amount of blood that they only use in key areas, such as their eyes, and their sprinting muscles. By heating these areas, it ensures that they are warmed up and ready to go when they come upon prey. It is interesting to think that with such a similar body plan and lifestyle to these Fish, the Ichthyosaurs may have also been convergent in their ability to warm their blood.

Just as there is an ongoing discussion about whether Dinosaurs were endothermic, producing their own heat, or ectothermic, relying on external temperatures like most Reptiles, there is a comparable question about marine Reptiles.

Do we have any proof that Ichthyosaurs may have been at least partially endothermic?

Unfortunately not, but we do have some clues.

1. Large animals, by virtue of their size alone, are better at retaining internal heat created by basic body functions. Small animals lose body heat faster than large ones, because they have more surface area to lose heat through, relative to the volume of their bodies.
2. Another clue comes from the microstructure of the limb bones in some Ichthyosaur species, which reveal growth patterns like the rings on a tree that indicate a high rate of bone growth. This growth pattern is characteristic of warm-blooded animals.
3. Finally, the ability to give live birth is another hint that Ichthyosaurs were endothermic. In order to have the embryos develop to term, they must be kept at a constant temperature. Unlike endothermic animals that are continuously warming their blood, it is difficult for ectothermic animals to maintain a constant internal temperature, because they are so reliant on the variable temperature conditions around them. We know that Ichthyosaurs gave birth to live young, meaning they must have had some way to maintain relatively consistent body temperature.

2.2.6 Reproduction

Ichthyosaurs seem splendidly adapted for swimming, but they would probably have been as helpless on land as a stranded Whale. In terms of reproduction, Ichthyosaurs got around this problem by giving live birth to up to 12 babies, instead of laying eggs on land. Evidence of live birth in Ichthyosaurs was actually discovered very early.

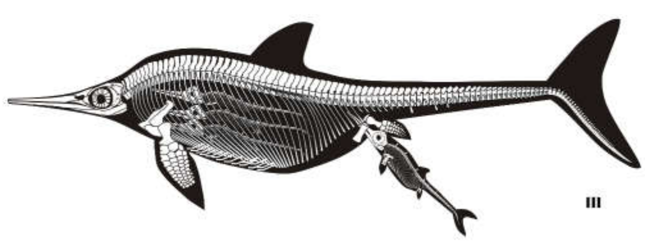


Illustration 64: Derived Ichthyooptergian with an embryo in birth position

In 1846, a specimen was found with a tiny Ichthyosaur skeleton protruding from the body of a much larger one, prompting scientists to look at other Ichthyosaurs that had been found with smaller skeletons inside. The tiny skeletons were found in the pelvic region and not in the stomach. It became clear that these were fetuses and that Ichthyosaurs were viviparous, which means they gave birth to live young. A difficult birth could have resulted in the death of the mother and her associated fetuses, accounting for the fossils that appear to show the mother in the process of giving birth. Another explanation for these partially expelled fetuses is that if the mother died before giving birth, the build up of gases inside her decomposing body could provide enough pressure to partially force out the infants. This is a phenomenon seen in beached Whales today.

2.2.7 Social Behavior

Further clues about Ichthyosaur social behavior can be found in an Ichthyosaur bone bed that preserves evidence of a mass death. There is a unique site in Nevada that preserves a bone bed full of 15 m long Shonisaurs. What is interesting about it is that all 40 of these animals are pointing in the same direction and are partially articulated, but incomplete.

Which scenario do you think could explain this?

Check all the answers you think apply.

A. A giant predator took bites out of all of them

B. They were trapped under sea ice

C. They were stranded on the beach

D. They were poisoned by toxic Fish

Finding so many articulated Ichthyosaur skeletons together indicates that they probably died at the same time. It is extremely unlikely that a predator killed them all at once; therefore, A is incorrect. In addition, the Mesozoic climate was very warm and no sea ice existed; therefore, B is incorrect.

It is possible that they will have been stranded on the beach, as sometimes happens with Whales today, therefore, **C** is possibly correct. However, it was later discovered that these rocks were from the open Ocean; therefore, stranding is unlikely.

Another suggestion is that they may have been poisoned by infected Fish. Today, toxic microorganisms called dinoflagellates can sometimes have a season where they are unusually abundant. They infect large numbers of Fish, and if a predator eats too many, they can be poisoned and die. This phenomenon is called a red tide and is a cause of some mass strandings seen in Whales today; therefore, **D** is also potentially correct. Either way, finding so many Ichthyosaurs together suggests that they were gregarious, living and sometimes dying in groups. **C** and **D** are the most correct answers.

2.3 Conclusion

As you have seen, Ichthyosaurs were splendidly evolved to overcome the aquatic problem. Even the earliest Ichthyopterygians were very distinctive Reptiles, completely adapted to marine life. Their hunting armament included large, sensitive eyes, and long snouts filled with small, pointy teeth, perfect for grasping slippery prey. Strong tails propelled their elongate fusiform bodies through the water at high speeds, and two pairs of flippers kept them going in the right direction.

They probably hunted deep in the water, diving in search of prey that is more abundant. It is likely they maintained a very high metabolism, possibly assisted by some endothermic capabilities. Being unable to leave the water, Ichthyosaurs were naturally viviparous, giving birth to live young, which may have been raised in family groups.

This first major group of marine Reptiles is a classic example of convergence, where the same function results in a similar form across evolutionary history. Let us now dive into the evolutionary history of Ichthyosaurs in order to develop an understanding of how their aquatic adaptations enable them to rule the Oceans for nearly 150,000,000 y.

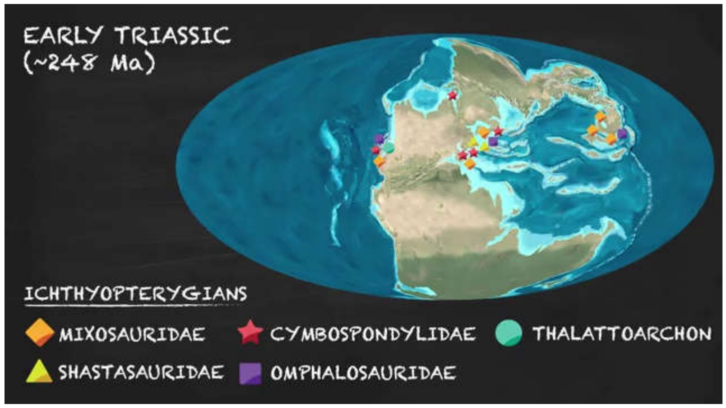
3 Ichthyopterygian Distribution Through Space And Time

3.1 Triassic

In this lesson, and the two that follow, we will conclude by exploring the distribution of marine Reptiles through space and time, by focusing on the localities where their fossils are found today. Ichthyopterygians and their closest relatives first appear during the Early-Triassic, about 248,000,000 y ago. The globe looked vastly different at this time, with Oceans flooding continents and forming shallow seas.

Ichthyopterygians diversified in these shallow seas and spread along coastal waterways quickly evolving morphological **disparity** or variations in body plan, which was greatest during the Late-Triassic. An extinction event at the end of the Triassic possibly linked to sea level fluctuations reduced the number of lineages that survived into the Jurassic. The species that did survive diversified again, into multiple groups of strong oceanic cruisers, before the entire group went extinct in the early part of the Late-Cretaceous.

3.1.1 Early-Triassic



Let us discuss the oldest know Ichthyosaurs. These fossils come from the Early-Triassic, and we know nothing about the evolutionary transition from their terrestrial ancestors, since all of the oldest Ichthyopterygians fossils we have discovered are already fully adapted to an aquatic lifestyle, and we have never found any intermediate forms, or terrestrial Proto-Ichthyosaurs. We do not know exactly where Ichthyopterygians originated, because Early-Triassic species are found all over the World, in Japan, from Eastern China to British Columbia, and the Svalbard Islands in the North Atlantic. No transitional early Ichthyopterygian has been found.

3.1.1.1 Transitional Characteristics

Which of the following characteristics do you think a transitional early Ichthyopterygian might have?

Select all that you think might apply.

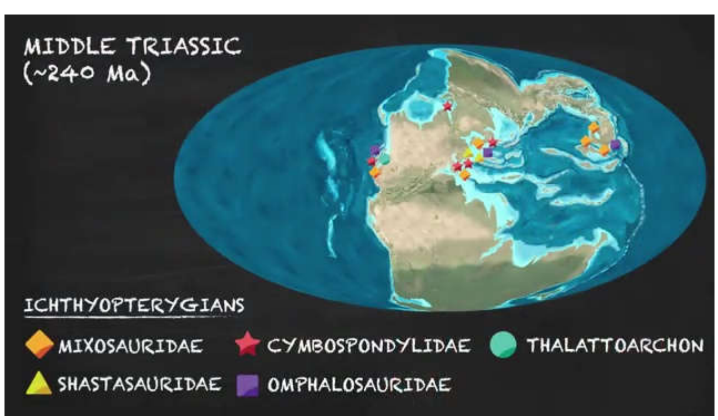
A. Long bodies
B. A blowhole
C. Carnivorous
D. Large orbits

Ichthyopterygians are descended from terrestrial Tetrapods that do not have blowholes. Even the most derived Ichthyosaurs have nares near their eyes, not on top of their head. Therefore, B is incorrect.

Large eyes are an adaptation for low light conditions; therefore, it is unlikely that early Ichthyosaurs would have the large orbits seen in later species that lived in the open Ocean; therefore, D is incorrect.

However, early Ichthyosaurs would likely have been long slender and carnivorous. This body shape and lifestyle are typical of most early transitional forms of Amniotes that returned to the water. The description also matches the earliest Ichthyopterygians that we HAVE found, like *Grippia*. It is likely that their ancestors were similar; therefore, **A** and **C** are correct.

3.1.2 Middle-Triassic



About 8,000,000 y into the Triassic period, during the Middle-Triassic, the first true Ichthyosaurs evolved, including a large bodied Ichthyosaur *Thalattoarchon*.

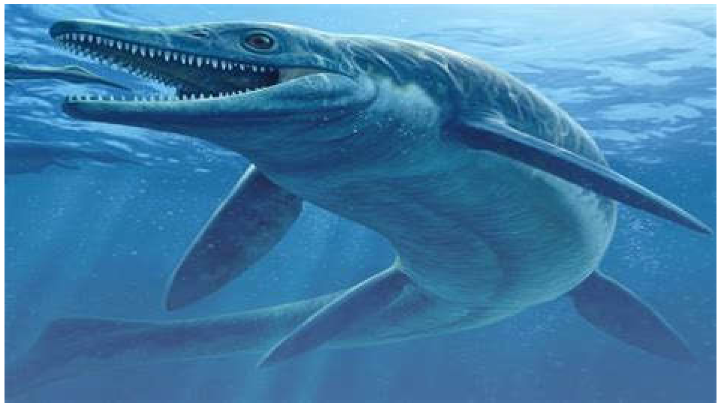


Illustration 65: *Thalattoarchon saurophagis* (Live restoration)

Thalattoarchon was one of the first apex predators in the Mesozoic and occupied the top rung of its food chain, consuming prey such as small marine Reptiles, Sharks, and Fish. Since large apex predators can only evolve if there is large prey for them to eat, the presence of *Thalattoarchon* in the Fossil record shows that marine ecosystems must have largely recovered from the End-Permian extinction, which had eliminated about 90 % of all life on Earth about 8,000,000 y earlier.

The Middle-Triassic represents the peak in Ichthyosaur species diversity and worldwide distribution. There were many different species with disparate morphologies. It is clear that these diverse animals could only have coexisted by specializing on different foods, and occupying different **niches** or roles in their community.

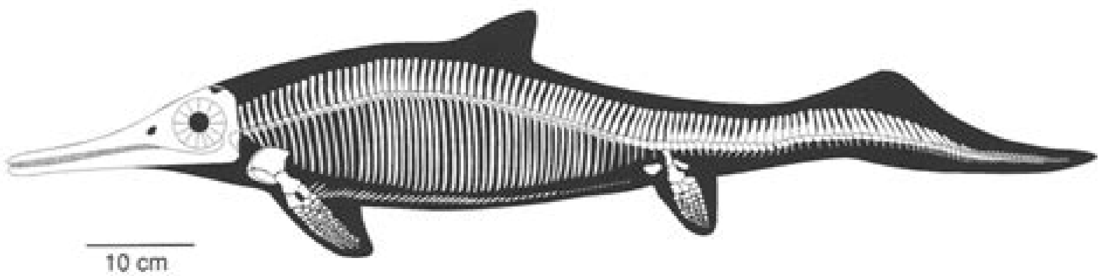


Illustration 66: *Mixosaurus* (Fossil)

One of the most abundant groups at this time was the Mixosauridae, particularly the 1 – 2 m long *Mixosaurus*. Mixosaurids have been found all across the Northern and Southern Hemispheres including Central Europe, the Svalbard Islands, Western North America, and even Indonesia. This suggests that in addition to being abundant, it was one of the most widespread of all Ichthyosaur groups. Although their tails were not as advanced as later Ichthyosaurs, Middle-Triassic species had evolved in more compact and fish-like shape, indicating they were faster swimmers than their Early-Triassic relatives, and this probably made their worldwide distribution possible.

3.1.3 Late-Triassic

Illustration 67*: Shonisaurus sikanniensis* (Fossil)

By the Late-Triassic, Ichthyosaurs reached their peak size with imposing giants like *Shonisaurus* and *Shastasaurus* dominating the Oceans. *Shonisaurus sikanniensis* was the largest of all known marine Reptiles at 21 m in length. Other species of *Shonisaurus* and *Shastasaurus* were still huge, in the range of 10 – 15 m. Fossils of these giant beasts have been found in China, the US, and Canada. Late-Triassic Ichthyosaurs are well represented by discoveries from the Pardonet Formation in the Pink Mountains of British Columbia. Dozens of Ichthyosaurs have been found here, sometimes, by helicopter pilots as they fly overhead.

Many of these Late-Triassic finds have been various species of *Shastasaurus*, including a new genus called *Metashastasaurus*, and the enormous *Shonisaurus sikanniensis* found near the Sikanni Chief River. The skull of this massive animal is 3.5 m long, and the largest piece of the Fossil weighs over 4,000 kg. The Fossil is so massive that it had to be airlifted using a cargo helicopter.

The end of the Triassic is marked by another mass extinction event, although this one was far less severe than the End-Permian extinction. This mass extinction might have been triggered by the break up of the super continent Pangaea, and is one of the most significant points in the evolution of the Ichthyosaurus. It represents an **evolutionary bottleneck** for the group.

3.1.3.1 Evolutionary Bottleneck

What do you think we might mean by the term evolutionary bottleneck? Choose all that apply. As a hint, think about what a bottleneck refers to in traffic, engineering, or software.

A. A place where a herd of animals is stuck

B. A reduction of species number, diversity, or disparity

C. A decrease in the average number of offspring

D. A drastic change in the environmental conditions

If you hear the term bottleneck in engineering, software, or in your morning traffic report, it refers to a point of congestion where the performance of the system is limited by a small number of components. When we talk about evolutionary bottlenecks, we are referring to a point in the evolution of a lineage where the number of individuals crashes, causing a decrease in species diversity, disparity, abundance, range, significance, or any combination of these. Therefore, **B** is the correct answer here.

A decrease in the number of offspring or a drastic change in environmental conditions could cause a decline in populations that could eventually lead to an evolutionary bottleneck, but they are not bottlenecks by themselves. Therefore, C and D are incorrect.

A place where a herd of animals gets stuck could correspond to a geographical bottleneck, kind of like when a long line of cars get stuck on the highway when it is blocked by construction, but it is not an evolutionary bottleneck. Therefore, A is also incorrect.

During the End Triassic extinction event, most Ichthyosaur taxa went extinct. Only two lineages that evolved at the very end of the period survive the extinction event. *Leptonectes* and *Ichthyosaurus* lived on to become the first in a new wave of Ichthyosaurs that evolve after this extinction. These early members of the Parvipelvia quickly achieved greater number and almost as much species diversity as all the Ichthyosaur families of the Triassic. However, they showed low morphological disparity, while the Triassic was populated by Ichthyosaurs with a variety of body shapes, including Lizard-like, Fish-like, and Whale-size forms, only small and medium-sized Dolphin-like Parvipelvian Ichthyosaurs were present in the Jurassic period.

3.1.3.2 Three Niches

In the Triassic, Ichthyosaurs occupied three niches; Fish-eating piscivores, Mollusk-crushing durophages, and predators at the top of the food chain.

3.2 Jurassic

3.2.1 Early Jurassic

After the evolutionary bottleneck, caused by the End-Triassic extinction, Ichthyosaurs only occupied one of these niches.

Which one do you think it was?

A. Fish eater

B. Durophage

C. Apex predator

Ichthyosaurs of the Triassic period had a variety of diets, while all the Jurassic Ichthyosaurs were open-Ocean Fish and Squid eaters, whose bodies were specialized to pursue their prey at high speeds. Some of the roles previously occupied by Ichthyopterygians in the Triassic seem to have been taken over in the Jurassic by marine Crocodilians, Sauropterygians, Sharks, and bony Fishes. Therefore, after the End Triassic extinction in the Jurassic Period, the only niche that Ichthyosaurs occupied was the open-Ocean Fish eater. Thalattosuchians, Sharks, bony Fish, and Sauropterygians diversified to fill the empty niches. Answer **A** is correct.

Illustration 68: Lyme Regis

An early example of the Early-Jurassic environment can be found at Lyme Regis on the Southwest coast of England, which is one of the most famous in best-preserved early Jurassic Reptile sites in the World. In these seaside cliffs, many remains of well-preserved, complete specimens can be found. Many of the earliest discoveries of prehistoric reptile remains were made in this area. Most notably, those discovered by a young woman named **Mary Anning,** who likely inspired the tongue twister; she sells seashells by the seashore.

Mary and her brother were not the first to find fossils of Ichthyosaurs. Earlier discoveries can be traced all the way back to the 1600^s. However, these earlier discoveries were thought to be Fish or Alligators. Mary's discoveries revealed that Ichthyosaurs were actually a unique group of Reptiles and caused scientists to consider the concept of extinction.

Illustration 69: Lower Lias

The Fossil deposits that Mary Anning explored were part of a Fossil-rich layer of rocks called the Lower Lias, which formed during the earliest Jurassic. Exposed strata from that time, from both Southern England and Belgium, contained fossils of Parvipelvian Ichthyosaurs, such as *Temnodontosaurus* and *Ichthyosaurus*, Leptopterygids, like *Excalibosaurus* and *Leptonectes* with their elongate swordfish-like snouts are also found in these localities.

Illustration 70: Holzmaden Quarry

Another of the most famous Ichthyosaur localities in the World is Holzmaden in Southern Germany. The Holzmaden oil shales exquisitely preserved an amazing variety of Ichthyosaurs from the end of the Early-Jurassic. Thousands of perfectly preserved fossils, particularly of *Temnodontosaurus* and *Stenopterygius* have been found here, including many of the most famous examples of pregnant females.

Illustration 71: *Stenopterygius quadriscissus* -giving birth (Holzmaden Fossil))

The sheer number of pregnant females found here suggests that this area may have served as a breeding or birthing ground for Ichthyosaurs similar to some of the shallow near-shore areas frequented by Grey Whales, Blue Whales, and Humpback Whales today.

Illustration 72: *Lepidotes elvensis* (Fossil)

Holzmaden is also famous for another reason. Most of the time fossils consist of bones, shells, teeth, and other hard parts. However, some localities provide us with some exceptional fossils. The fossils of Holzmaden preserved soft tissue like skin, tendons, and even organs in exquisite detail.

3.2.1.1 Soft Tissue Fossilization

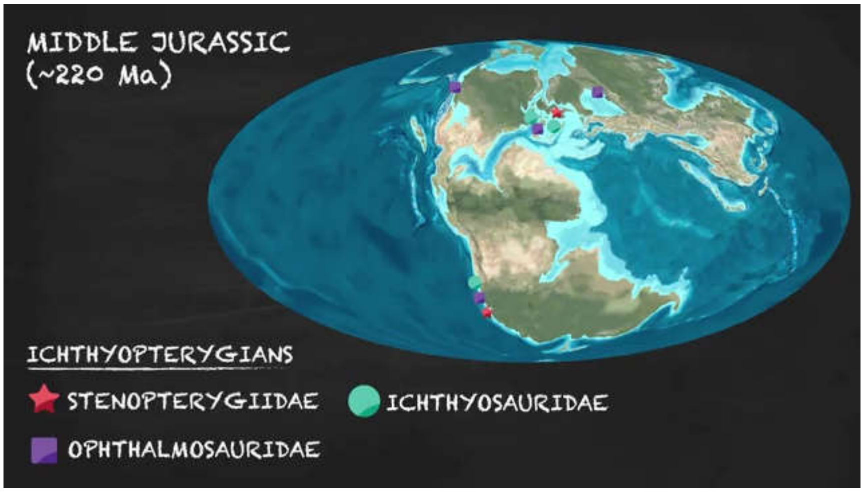
Why are fossils that preserve soft tissues so important to paleontologists? Check all that you think apply.

- **A.** They can tell about body shape
- **B.** They can tell us about mating behavior
- **C.** They can tell us what color they were
- **D.** They can tell us about internal organs

Our knowledge of the muscles, skin, eyes, and other soft tissues of long extinct animals usually consists of educated guesses. For example, we can use the size and shape of the interior of the skull to tell us things about the brain. The fossils of Holzmaden provide some of the best evidence paleontologists have to determine overall body shapes of Ichthyosaurs, because the soft tissues of the body wall, flukes, and flippers are remarkably preserved here as a dark film of carbon around the skeleton.

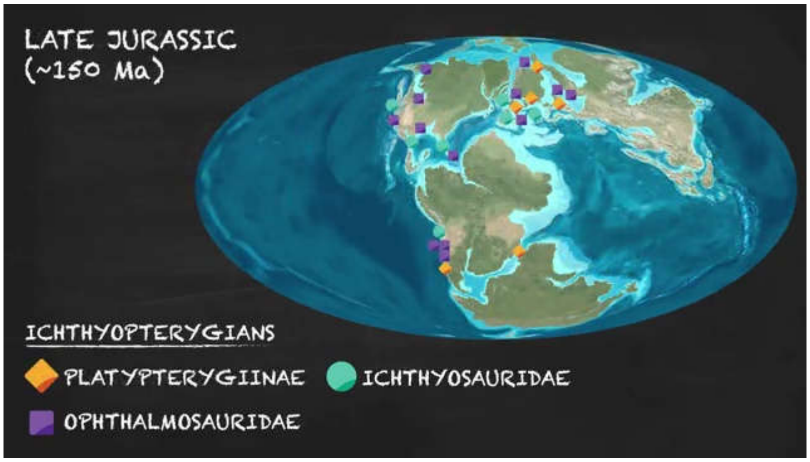
These fossils also occasionally preserve parts of the internal organs, which can tell us a lot about the physiology and internal anatomy of these animals. With information like this, paleontologists can make more educated guesses about behaviors involved with hunting and movement. Unfortunately, they cannot tell us anything about mating behavior or the color of the animals. Therefore, the correct answers here are **A** and **D**.

3.2.2 Middle-Jurassic



Ichthyosaur species diversity starts to decline during the Middle-Jurassic, and their fossils are not very abundant from this time. The huge-eyed Thunnosaurian genus, *Ophthalmosaurus*, first evolved and became abundant during the Middle-Jurassic. As far as we know, this was one of the only taxa of Ichthyosaurid swimming in the Middle-Jurassic seas.

3.2.3 Late Jurassic



By the Late-Jurassic, the only surviving lineages of Ichthyopterygians were the Thunnosauria. *Ophthalmosaurus* survived into the Late-Jurassic, and its fossils are common in the Oxford Clay of England, and in the Sundance formation of the Western US. However, both of these localities preserve no other Ichthyosaur genera.

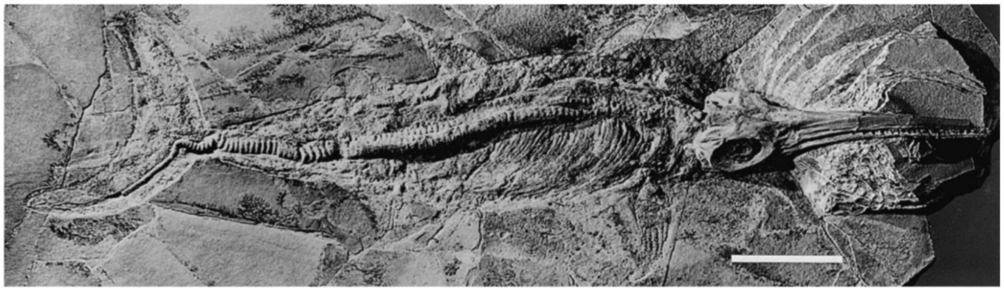


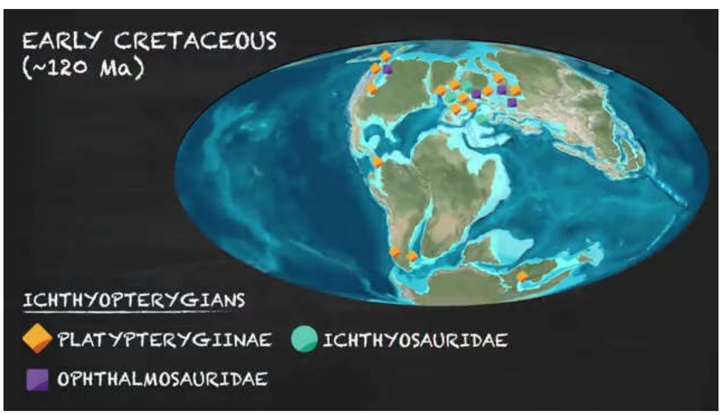
Illustration 73: *Aegirosaurus leptospondylus* (Solnhofen Fossil)

The Solnhofen limestone of Germany, where *Archaeopteryx* comes from, has produced an exceptional specimen of the Ichthyosaur *Aegirosaurus*. Impressions of its soft tissues were preserved all around the body in showed the typical crescent-shaped tail, and four flipper-like limbs. From the preserved impressions, we know that the graceful forelimbs were long and narrow, and the hind limbs were shorter and broader. In this specimen, there were also impressions interpreted as minute scales covering the whole body. Impressions of tiny fibers were also found in some specimens that are similar to collagen structures found in marine Mammals and Sharks, which help keep the skin tight, smooth, and hydrodynamic.

3.3 Cretaceous

3.3.1 Early Cretaceous

Our understanding of Cretaceous Ichthyosaurs has greatly improved in the last few years. A significant extinction event for marine organisms occurred at the Jurassic-Cretaceous boundary, possibly because of a climate change. Until very recently, it was thought that most Ichthyosaur lineages went extinct at the end of the Jurassic, leaving only a single genus, *Platypterygius*, in the Cretaceous. The general consensus was that the Cretaceous Ichthyosaurs were not very diverse, and gradually tapered off until they just disappeared completely around the Middle-Cretaceous. New discoveries and new studies, however, are changing our ideas about the last Ichthyosaurs.



Isolated and fragmentary Ichthyosaur remains were known from Early-Cretaceous strata across Europe, but many of these fossils could not be precisely identified. Since 2000, new fossils have been found, and specimens in museum collections have been reevaluated. They have revealed that Ichthyosaurs from this time were more diverse than paleontologists understood just a decade ago. New species have been found across Europe, Argentina, Iraq, and Russia. All the new species belong to the Thunnosauria, and most of them are closely related to either *Ophthalmosaurus* or *Platypterygius*.

Illustration 74: *Athatbascasaurus bitumineus* (Fossil)

Ophthalmosaurs and Platypterygians are also relatively abundant in Canada from the time when the Western Interior Sea bisected North America. Two new species of Ophthalmosaurs have also been found in Canadian Middle-Cretaceous strata. One is *Athatbascasaurus bitumineus*, which was found in an oil sand mine in Northern Alberta. *Bitumineus*, which is a species name, was inspired because this specimen still has tar, or bitumen, oozing out of its bones.

Illustration 75: *Maiaspondylus lindoei* (Live restoration)

The other new Ophthalmosaur is *Maiaspondylus lindoei*. This specimen was found in the Northwest Territories. *Maiaspondylus* means good mother vertebrae, and it refers to the pair of preserved embryos found inside the mother, near her backbone. *Lindoei*, the species name, is in honor of the University of Alberta technician who discovered the fossils.

3.3.1.1 Supporting Hypothesis

The recent discoveries of many Early-Cretaceous Ichthyosaurs are changing the way paleontologists think about their extinction.

Which hypothesis do these discoveries support?

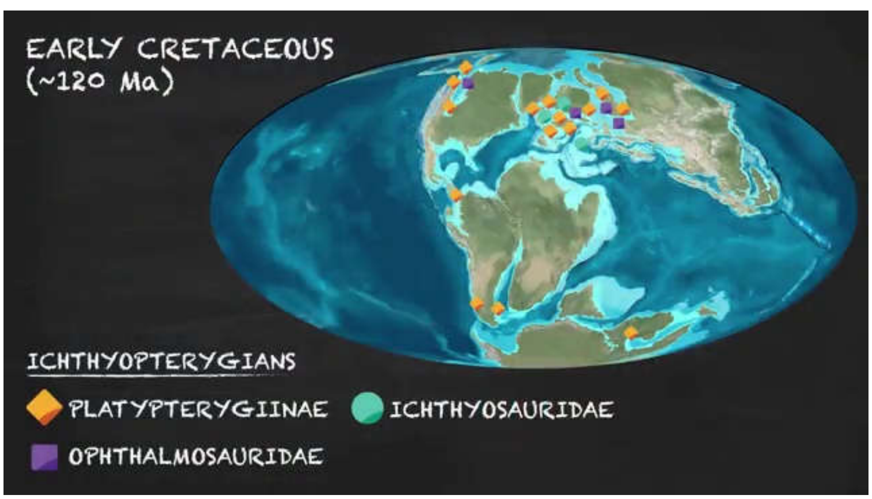
A. All species of Ichthyosaurs went extinct at the end of the Jurassic

B. Early Cretaceous Ichthyosaurs were few stragglers left over from a greater dynasty

C. There were many species of early Cretaceous Ichthyosaurs that occupied a variety of ecosystems

The unexpected species diversity of Cretaceous Ichthyosaurs supports the updated hypothesis that they were not just a few stragglers left over from a greater dynasty. The last Ichthyosaurs did not go extinct in the Jurassic. They were still relatively diverse and played important parts in their ecosystems. Therefore, the correct answer is **C**.

3.3.2 Mid-Cretaceous



By the Mid-Cretaceous Ichthyosaur diversity was dramatically reduced. *Platypterygius* is the only representative of the Ichthyosaur lineage that has been found in any strata younger than 100,000,000 y old. These remaining Ichthyosaurs still had an extensive range across the Northern Hemisphere. However, it appears that early paleontologists were correct in thinking that Ichthyosaurs died off in the Mid-Cretaceous, long before the extinction event that has killed other marine Reptiles and the Dinosaurs.

3.4 Extinction

Why did the Ichthyosaurs go extinct in the middle of the Cretaceous Period about 93,000,000 y ago? Why did they not survive until the End-Cretaceous extinction like the Plesiosaurs, Mosasaurs, and Dinosaurs?

When we thought that Cretaceous Ichthyosaurs were just a few stragglers, it seemed like maybe other marine Reptiles slowly replaced them. It is an intriguing coincidence that Mosasaurs originated around the same time the Ichthyosaurs finally went extinct; therefore, it is been proposed that the Mosasaurs out competed the Ichthyosaurs for resources.

However, the earliest Mosasaurs were quite small, and would have lived near shore; therefore, it is unlikely that they came into direct conflict with the Ocean cruising *Platypterygius*. The answer to Ichthyosaur extinction will require paleontologists to find additional fossils that will allow a better understanding of Mid-Cretaceous Ocean ecosystem dynamics.

3.5 Conclusion

The Ichthyosaurs are among the most specialized Reptiles that have ever lived. They were superbly adapted for life in the Oceans with their long tooth-studded mouth, large eyes, powerful tails, and two sets of steering flippers. Ichthyopterygians came in all sizes from small to extra large, but most solved the aquatic problem by converging on a similar body plan to modern Tuna.

They may even have been endothermic. The limitations imposed by having to lay eggs on land were bypassed by giving birth to live young, and it is possible that they raised these young in social groups. They were rulers of the Oceans for nearly 150,000,000 y.

What happened to them?

We can only speculate. Perhaps, the answers to their demise lie in studying the other marine Reptiles that shared the Oceans with them, the Plesiosaurs and Mosasaurs that we will learn about in the following lessons.

Sauropterygians

1 Sauropterygian Systematics

Illustration 76: Sauropterygians (Live restoration)

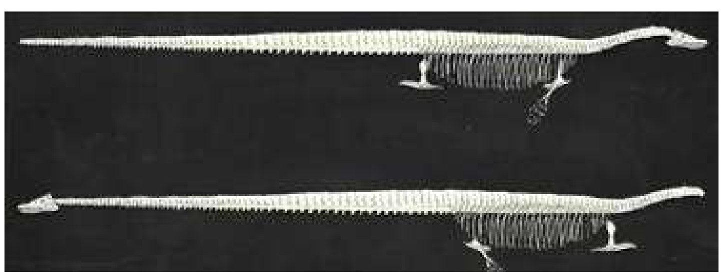
In the last lesson, we looked at the characteristics and diversity of Ichthyosaurs and their close relatives. In this lesson, we are going to explore another group of aquatic Reptiles, the Sauropterygians. The Sauropterygians are best known for their derived members, the Plesiosaurs. Like the Ichthyosaurs, the first Sauropterygians appeared in the Early-Triassic. These early forms were small, semi-aquatic animals with small heads, elongate bodies, and four limbs adapted for paddling around in shallow water. By the End-Triassic, they had grown into fully aquatic animals, incapable of returning to shore. Throughout the Jurassic and the Cretaceous, these Reptiles developed a large number of diverse specialized body plans adapted for life in the water. The last members went extinct with the Dinosaurs at the End-Cretaceous mass extinction. We will begin with the basic questions about these animals:

What were they and what did they look like?

1.1 Sauropterygian Relationship To Other Diapsids

1.1.1 Plesiosaur Head Location

Based on other aquatic Tetrapods you have seen so far in this course, where do you think the head was positioned on this animal?



Did it have a short neck and a long tail or a long neck and a short tail?

If you pick the Plesiosaur with the short neck and long tail you chose the arrangement that is most convergent among aquatic Tetrapods. Many aquatic Tetrapods you have seen so far, such as Ichthyosaurs, Thalattosuchians, and Whales lengthen their tails for use as a propulsive structure. However, the Plesiosaurs evolved a different solution to the aquatic problem. Their tails got quite short, and in some cases their necks grew to extraordinary lengths. Therefore, the long neck, short tail configuration is correct here.

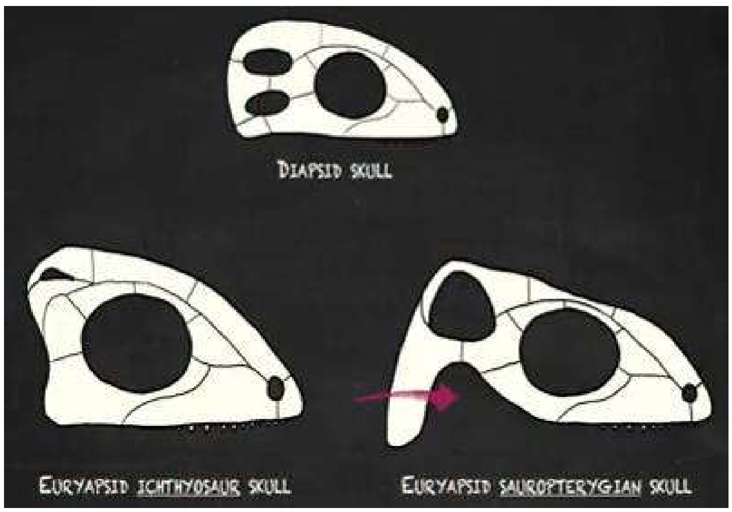
Nevertheless, do not feel like you missed something if you got it wrong. One of the most famous paleontologists in history, Edward Drinker Cope also put the head on the wrong end of a Plesiosaur specimen before putting it on display. When his bitter rival, Professor Othniel Charles Marsh, gleefully pointed out his error, Cope was so embarrassed he blamed a colleague at the museum for his mistake.

The Sauropterygia includes the long neck Plesiosaurs and a whole host of other interesting Mesozoic marine Reptiles that do not usually receive as much attention in the popular media. Like the Ichthyopterygians, Sauropterygians have been somewhat hard to place on the tree of life. The general consensus today is that Sauropterygians are a separate lineage of Diapsids, but in some phylogenetic analyses, they are grouped in the Lepidosauromorpha.

1.2 Sauropterygian Diagnostic Characters

Illustration 77: Plesiosaur skull showing the Euryapsid condition

The name Sauropterygian means **winged Lizard**, which refers to the paddle-like limbs common to the group. Sauropterygian share several other characteristics in their skull and skeleton. Sauropterygian skulls usually have retracted nares close to the orbits, and this is an adaptation for air breathing swimmers.



Like Ichthyosaurs, they have Euryapsid skulls, meaning the lower temporal fenestra has been lost and only the upper one remains. However, the Euryapsid condition has been achieved very differently in each group.

Think back to the lesson on Ichthyosaurs. These animals evolved the Euryapsid condition due to a reduction in the postorbital region. In Sauropterygians the Euryapsid morphology results from the loss of the bony bar that forms the bottom edge of the lower temporal fenestra. This leaves them with an archlike space and a complete upper temporal fenestra.

The loss of the lower fenestra has been used to suggest common ancestry of Sauropterygians, Ichthyopterygians, and Thalattosaurs, but it is now understood that the lower fenestra was lost independently in these groups.

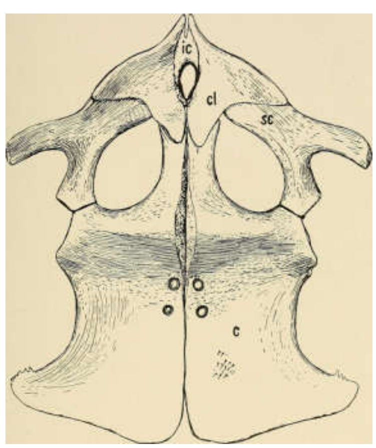
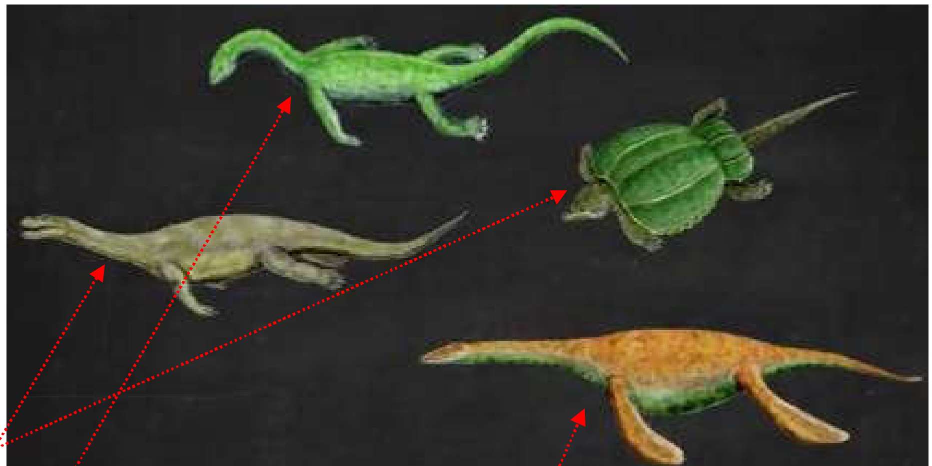


Illustration 78: Plesiosaur pectoral girdle as seen from above, showing scapula extending to the clavicle

Sauropterygians can also be identified by their distinctive pectorial girdle. The scapula, or shoulder blade, partially overlaps the outside of the clavicles or collarbones, while in other Amniotes the clavicles overlap the outside of the scapula. Those that study the Sauropterygians are still not sure why this adaptation occurred and which function it provided. Despite these shared features, Sauropterygians evolved into a wide variety of body shapes, enabling them to occupy many different ecological niches throughout their evolutionary history. We will explore these in more detail next.

As we mentioned, Sauropterygians came in various shapes and sizes, which indicates that they had a variety of ecological specializations. See if you can apply what you have already learned in the past two lessons.

Decide whether each of these basal Sauropterygians would have been fully aquatic, semi-aquatic or terrestrial.



Let us go through each of these basal Sauropterygians to see where they should be placed. First, the Placodont, do not let the legs fool you. Placodonts with their compressed bodies and unique toothplates were specialized bottom feeders in shallow marine settings. Even though it may look like Placodonts might have been able to climb out and walk, paleontologists think that their entire life cycle could have been performed in the water, making them **aquatic**.

Nothosaurs did not have the specialized flippers of strong swimmers; therefore, we think they were likely **semi-aquatic**.

With their highly derived flippers, it is likely that Pistosaurs were **aquatic** and could not have gone onto land at all.

Pachypleurosaurs, like the Nothosaurs, did not have the specialized flippers of strong swimmers. Additionally, Pachypleurosaurs had thickened bones, characteristics of animals that live in near shore settings. That means that the Pachypleurosaurs were most likely **semi-aquatic**.

As all this animals have some degree of aquatic adaptation none of this would have been fully terrestrial.

1.3 Sauropterygian Phylogeny

1.3.1 Sauropterygia

The Sauropterygian lineage spanned approximately 180,000,000 y, from the origin of the first members of the clade about 248,000,000 y ago in the Triassic, until the End-Cretaceous mass extinction 66,000,000 y ago. Even though uncertainty remains over their place in the Diapsid tree, the trends that eventually led to the derived Plesiosaurs is well understood.

1.3.2 Placodontia

Now let us go into more detail on these basal Sauropterygian groups. Let us begin our exploration of the major Sauropterygian groups with the most primitive aquatic form, the Placodonts. These animals first appeared in the Early- to Middle-Triassic during a period of global sea level rise. Placodonts tended to have one of two body plans, or **morphotypes**: some were barrel-shaped and others were wide and flattened. Both had fairly rigid bodies and must have used their webbed feet and laterally compressed tails to propel them through the water.

Placodonts were likely durophagous, feeding on hard-shelled Mollusks with their distinctive dental morphology. They had large, wide, and flattened teeth found not just along the edges of their jaws, but also across the roof of their mouths!

Illustration 79: *Placodus* (Fossil)

Placodus is a good example of some of the specialization of the Placodonts. It was 2 m long with a massive skull, gastralia, and spines down its back. It looked a bit like an over grown buck-toothed Iguana. It had large shovel-like teeth jutting forward out of its jaws and probably used them to pray shellfish off of underwater rocks, before crushing them like a nutcracker between the heavy plate-like teeth on its palate and lower jaw.

Illustration 80: *Henodus* (Fossil)

On the other end of the spectrum, *Henodus* was a flattened armored Placodont that was as long as it was wide. It had protective amour on its ventral and dorsal sides, composed of bony plates, covered in horn, and looked superficially similar to a Turtle. This is yet another good example of convergent evolution.

1.3.2.1 Baleen Feeding

The most intriguing thing about *Henodus* is that it was almost entirely toothless, but grooves in the jaw supported a baleen-like material, similar to filter-feeding Whales.

Like the baleen of today's Whales, it probably would have eaten zooplankton or small Fish. What is this kind of feeding called? If you are having problems determining which one you should select, think back to the lesson on Ichthyopterygian feeding.

A. Manipulation feeding

B. Lunge feeding

C. Ram feeding

Remember that manipulation feeding involves the animal using its teeth to bite, tear, or scrape its prey; therefore, A is incorrect.

Ram feeding and lunge feeding are both types of filter feeding, where small prey is filtered out of the water using specialized structures. In Fish, the prey is filtered out of the water using specialized structures on their gills. This is called ram feeding; therefore, C is incorrect.

Amniotes do not have gills, and therefore, they have to take in a mouthful of water and push it back out of specialized structures that have replaced their teeth. This is called lunge feeding; therefore, **B** is correct.

1.3.3 Nothosauroidea

Illustration 81: *Lariosaurus* (Fossil)

The next most derived group of Sauropterygians to evolve during the Triassic was the Nothosauroidea. They had slender bodies, long necks and tails, and webbed feet. They flourished in Europe during the Middle-Triassic and were probably able to come out of the water like modern Seals. Their nostrils were not at the tip of the nose like most Reptiles, but were set further back suggesting at least a semi-aquatic lifestyle.

1.3.4 Pachypleurosaurs

Illustration 82: *Keichosaurus* (Fossil)

The Pachypleurosaurs may have been a subgroup of Nothosaurs, a sister group to Nothosaurs, or more likely a series of species that lead towards more derived Sauropterygians, including the Nothosaurs and Plesiosaurs. Pachypleurosaur means **thick ribbed Lizard**, and the name reflects the thickened ribs of these Sauropterygians. They are found in European and Chinese deposits from the Middle-Triassic. They have a wide range of sizes from 20 cm to 4 m long.

Pachypleurosaur skeletons have poorly ossified limb girdles suggesting that they could not walk very well. However, the feet had not become specialized into flippers suggesting they probably moved by undulating their long tails. It is possible that the pachyostotic ribs provided neutral buoyancy and stability in the water column. They had small heads, moderately long necks, and small, cone-like teeth, which suggest they ate Fish.

1.3.5 Pistosauroidea

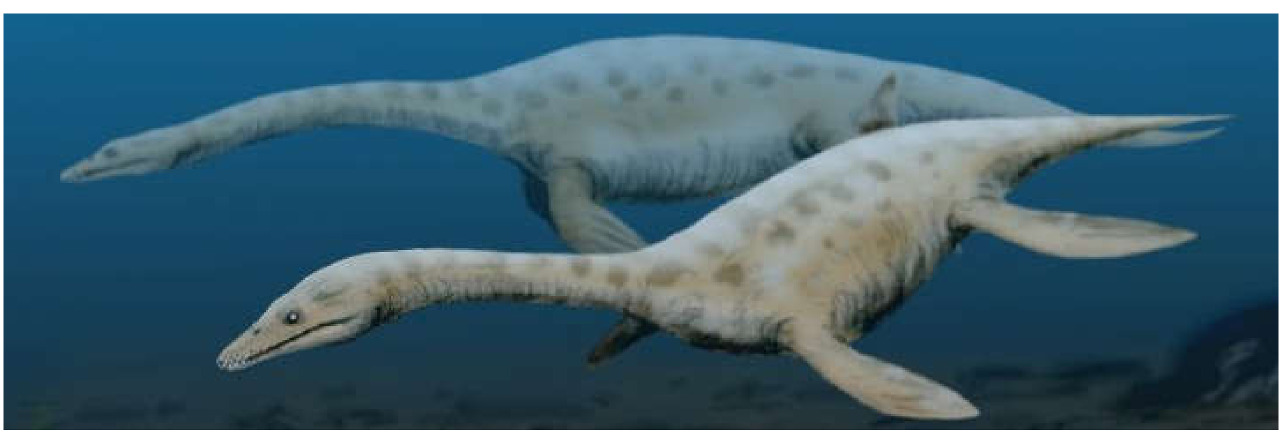


Illustration 83: *Augustasaurus hagdorni* (Live restoration)

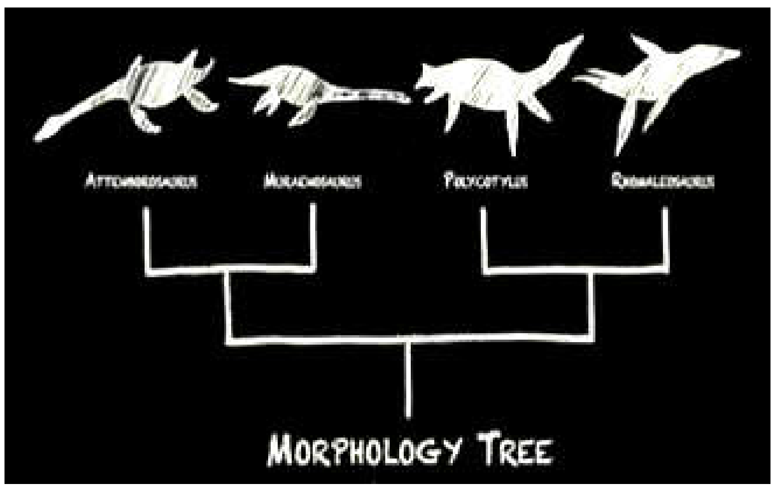
Pistosauroidea is thought to be the sister taxon of the derived Plesiosaurs. Only a few Pistosaurs have been found in Triassic strata, including localities in Germany and China, but these rare fossils suggest that Pistosaurs represent an intermediate form between the Nothosaurs and the Plesiosaurs. They had a Nothosaur-like body and a Plesiosaur-like head. Pistosaur limbs have wide, more expanded shoulder and hip girdles, and their fingers show some hyperphalangy. This indicates that Pistosaurs were better adapted to an aquatic life than the Nothosaurs and Pachypleurosaurs that came before them.

1.3.6 Plesiosauria

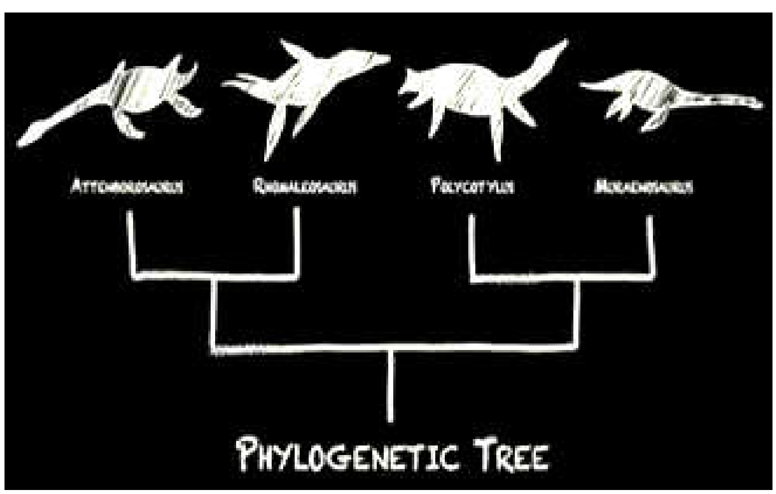
Placodonts, Pachypleurosaurs, Nothosaurs, and Pistosaurs show a huge variety of body plans and specializations and likely filled a wide array of niches in the Triassic Oceans. Similar to what you learned about Ichthyosaurs in the last lesson, the End-Triassic extinction event led to an extreme drop in Sauropterygian species diversity. Only one clade survived into the Jurassic, but this lone group of survivors went on to become very diverse and successful: the Plesiosaurs. The name Plesiosaur means **near reptile**, because it was recognized that they were more like Saurians, or Lizards, than the fish-like Ichthyosaurs. These creatures evolved into dominant roles in the Mesozoic seas, and were powerful predators that evolved around two basic body plans.

Based on what you know about how comparative morphology is used to infer phylogenetic relationships, we want you to think about which of these Sauropterygians are most closely related to each other.

If you were to group them into two pairs of sister groups, how would you do it? Would you group together the individuals with the small heads and long necks, and the animals with large heads and short necks?



If so, you would recreate the morphology base groups that paleontologist used for over a 150 y; the long necked **Plesiosauria** and the bigheaded **Pliosauria**. It seems like the most straightforward answer would be to group the fossils that most closely resemble each other, but when biology and millions of years of evolution are involved, the situation is not always that simple.



Detailed study of more subtle and complex characters, such as the structures of the bones in the skull and the limb girdles, suggest that the Plesiosaur lineage looks more like this. As you can see, the Pliosaur morphotype evolved multiple times. In addition, the Plesiosaurs with the extraordinary long necks associated with the Elasmosaur morphotype also appeared in numerous clades. Therefore, as we have discovered, these two morphotypes reflect the true relationships very poorly.

When paleontologists want to talk about groups of animals that look the same, but they are not related, we can talk about them by grouping them into morphotypes, or groups that look similar. In Plesiosaurs, there are two main morphotypes. The first are the **Pliosauromorphs**. These are the Plesiosaurids with a Pliosaur morphotype. They have short necks and big heads with jaws full of large teeth. The second morphotype are the **Elasmosauromorphs**, the Plesiosaurids with the extraordinarily long necks and small heads.

Notice that groups referring to morphology and not relationships always end in morph.

The Plesiosauria is a clade of derived Sauropterygians that is nested within **Pistosauria**. The Pistosauria is the clade composed of the Pistosauroidea and Plesiosauria. Fossils of a Plesiosauria have been found from Early-Jurassic through Late-Cretaceous strata. All members of this clade had four long narrow flippers connected to the limb girdles, which were modified into characteristically broad sheets of bone to which the powerful swimming muscles were attached.

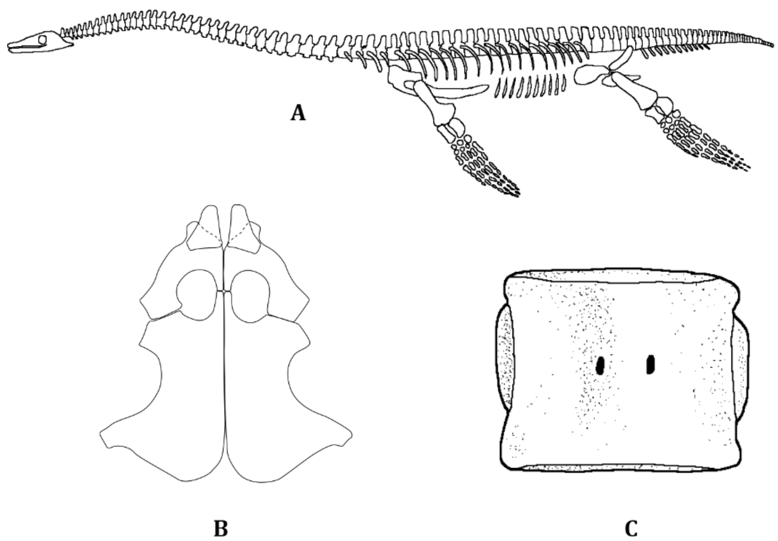


Illustration 84: Specific Plesiosaur diagnostic characteristics

A = Gastralia; B = Girdle; C = Vertebrae

Another **diagnostic character** of Plesiosaurs, which differentiates them from other marine Reptiles, is a pair of holes on the ventral surface of the cervical vertebrae. These holes are called the **subcentral foramina**, and they allowed the nerves to pass through. A final feature shared by Plesiosaurs is **Gastralia**. Along with the ribs, these bones would have enclosed the torso in a shield of internal body armor.

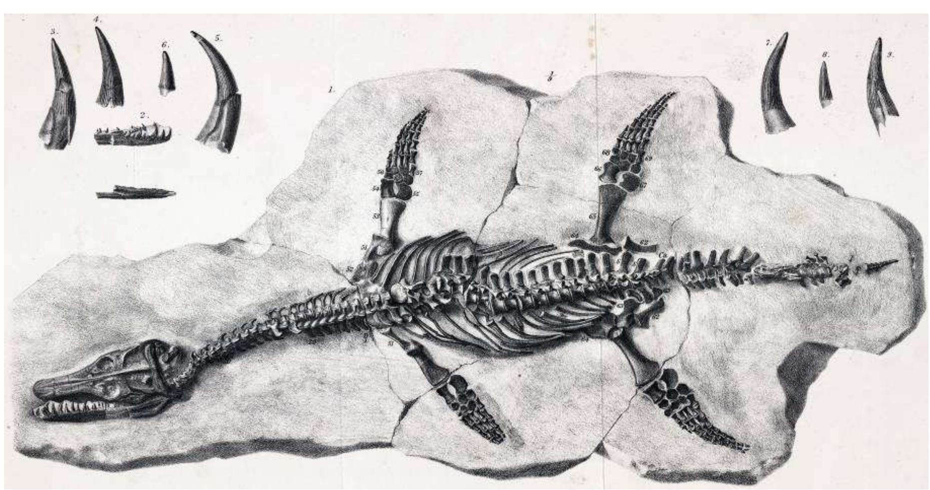
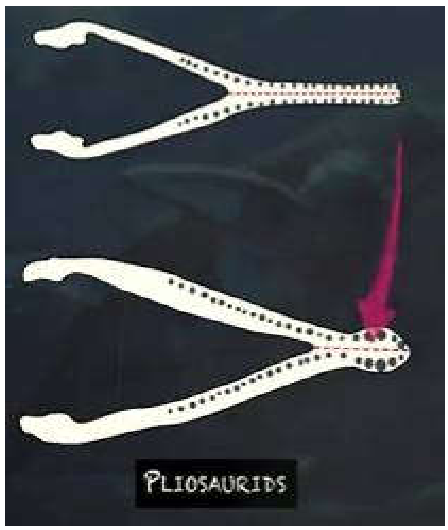


Illustration 85: *Archaeonectrus* (Fossil)

Archaeonectrus rostratus and *Attenborosaurus conybeari* are two primitive Plesiosaurs from the Early-Jurassic, that fit outside the two major Plesiosaur superfamilies, which we will introduce you to in a moment. They represent an intermediate form between the basal Sauropterygians we just looked at, and the derived taxa we will introduce you to next. Even though both of these species were probably fully aquatic they were not very specialized in any particular mode of life in the Ocean. For example, while the limbs of *Archaeonectrus* show some hyperphalangy, they are not particularly large relative to the rest of the body, especially when compared to later, more derived taxa.

1.3.7 Pliosauridae

On one side of the Plesiosaur lineage, is a clade called the Pliosauridae, which has the typical Pliosaur morphology. This group is composed of two main families: the primitive, Early- to Middle-Jurassic, Rhomaleosauridae, and the more derived Middle-Jurassic to Late-Cretaceous Pliosauroidea. All the Pliosauroids have a big skull and a short neck, and can be differentiated from other Pliosauromorphs by their lower jaws.



In Pliosaurids, the two halves of the lower jaw are connected by a short joint between the massive front few teeth. The jaws were wide like a spoon to support these powerful teeth.

1.3.8 Rhomaleosauridae

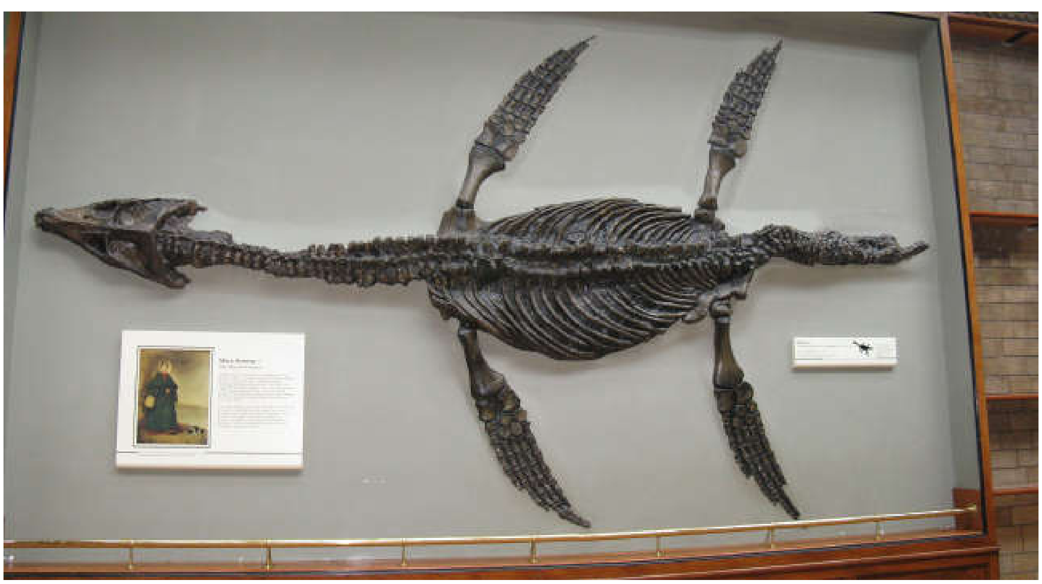


Illustration 86: *Rhomaleosaurus* (Fossil)

Species within Rhomaleosauridae looked similar to the more primitive *Archaeonectrus rostratus* and *Attenborosaurus conybeari*. They had relatively long necks with 25 - 30 cervical vertebrae. They had short snouts and a fairly long tail of about 37 vertebrae. More derived characters include very large flippers and correspondingly large limb girdles. These would have provided muscle attachment sites to power those massive limbs. Species belonging to the Pliosauridae had massive heads, with long snouts and reduced numbers of cervical vertebrae.

Illustration 87: *Liopleurodon* (Fossil)

Liopleurodon is probably the most famous genus of this clade. Its size has often been exaggerated in public media, but at 7 m it still was one of the largest predators in the Jurassic seas.

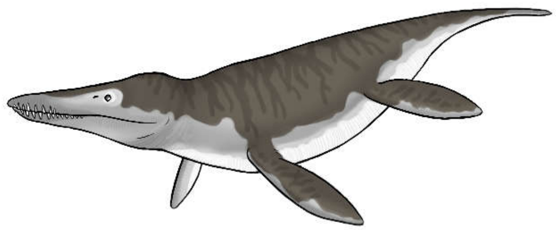


Illustration 88: *Kronosaurus* (Live restoration)

A true giant of the clade is the Australian *Kronosaurus queenslandicus*, named after the mythical titan who ate his children. *Kronosaurus* was 10 m in overall length. The crowns of its teeth could exceed 10 cm, but lacked the cutting edges of *Liopleurodon* and *Pliosaurus*; therefore, it likely had a different diet. Let us explore that now.

1.3.8.1 Tooth And Prey

Different large Pliosaurids had teeth that were specialized for eating specific prey items. Drag the prey items to the teeth that were best adapted to process that food.

These teeth might not look terribly different from each other, but they do have features that would have made each of them better specialized to handle certain prey items.

The left tooth looks halfway between a cut and a pierce tooth. It is long, which is good for trapping Fish and Squid, but it also has cutting edges; therefore, it would have been able to slice up prey. This tooth is from *Liopleurodon*, which ate large Fish, Squid, and maybe other marine Reptiles.

The middle tooth is definitely a cutting tooth. It has strong cutting edges; therefore, it would have been even better at piercing and slicing prey. It is from *Pliosaurus*, which ate large Fish and other marine Reptiles.

The right tooth is the largest, but it does not have cutting edges. It is long like a pierce tooth, but blunt and conical like a smash tooth. These teeth would have been good at immobilizing small prey, such as small marine Reptiles, Turtles, Fish, and Squid that the Pliosaurids could have swallowed whole. This tooth belongs to *Kronosaurus*. These diets are supported by the discovery of preserved stomach contents found with the fossils of these Pliosaurs.

1.3.9 Plesiosauroidea

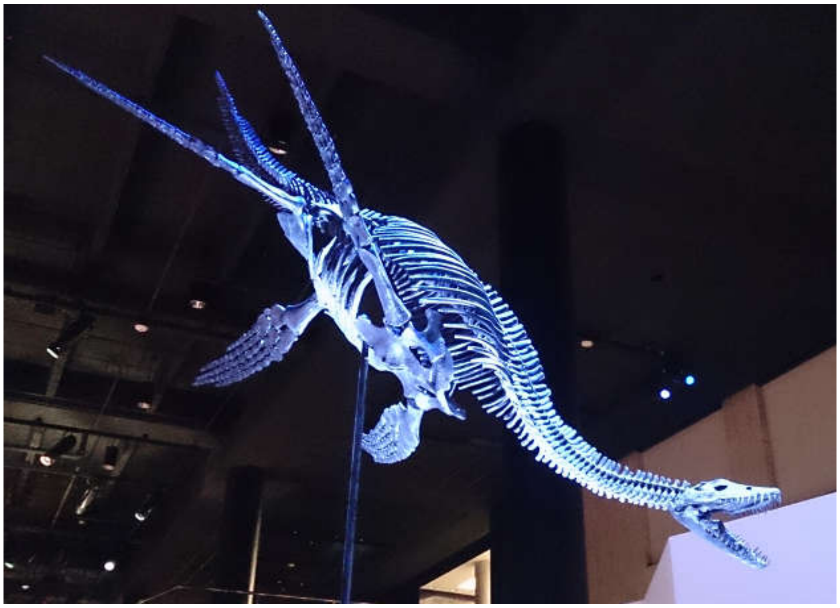


Illustration 89: *Plesiosaurus dolichodeirus* (Fossil)

All other species of Plesiosaurs fall into the **Plesiosauroidea**. This group shows a huge diversity in form, but all members can be identified by the lack of nasal bones, which are replaced by other bones in the skull.

Within this group, the family Plesiosauroidae is typified by the original Plesiosaur, *Plesiosaurus dolichodeirus*. Most early discoveries of Plesiosaur fossils were assigned to Plesiosaurus, which became a **wastebasket taxon**. A wastebasket taxon contains many unrelated species that being grouped together, because they look vaguely similar, or because scientists do not know where else to assign them. This means that the wastebasket taxon is not a true group, and therefore, each species within the wastebasket taxon needs to be critically examined to see if it actually belongs. This is the case for Plesiosaurus. Not all the early taxonomy has been checked; therefore, this clade is hard to define.

1.3.10 Elasmosauridae

On the opposite end of the morphology spectrum from the Pliosaurids is the **Elasmosauridae**. Species in this Cretaceous clade had 40 or more cervical vertebrae. Besides the long neck, Elasmosaurids can be identified by a wide indentation in the posterior edge of the pectoral girdle.

Illustration 90: *Elasmosaurus platyurus* (Fossil)

Possibly the most striking of the Plesiosaurs and certainly one of the most famous is *Elasmosaurus*, one of the longest known Plesiosaurs. Is at least 14 m long with over 7.5 m of neck, composed of 70 vertebrae, ending in a tiny head.

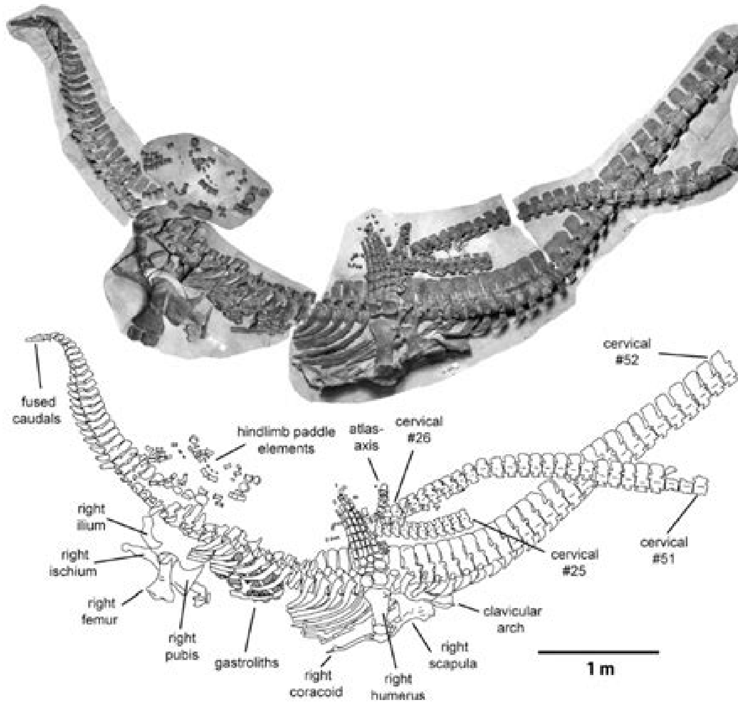


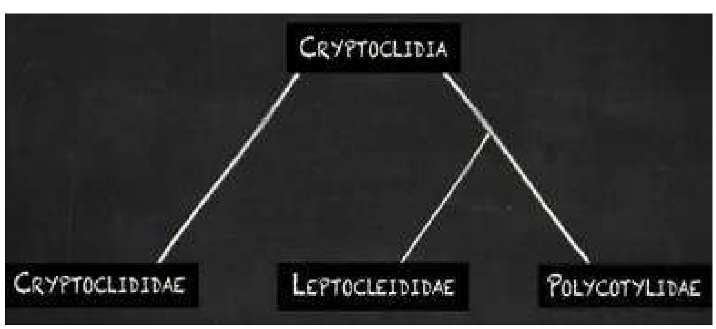
Illustration 91: ***Albertonectes vanderveldei*** **(Fossil)**

However, Elasmosaurus lost the title of most cervical vertebrae in 2012 with the discovery of *Albertonectes vanderveldei* in Alberta, Canada. The animal slightly smaller than Elasmosaurus has a neck of similar length with a whopping 76 cervical vertebrae.

1.3.11 Cryptoclidia

The **Cryptoclidia**, meaning hidden clavicles, are named for their most distinctive feature. Their small, practically invisible clavicles that lie hidden in shallow depressions of the inner surface of the front limb girdle. This clade is quite diverse. It contains numerous species, showing a huge variety of morphologies. In fact, all the Plesiosaur body plans from big heads to long necks can be found in one species of Cryptoclidid or another, just not taken to the extreme of the Pliosaurids or Elasmosaurids.

The wide range of morphologies in this group often led them to be misclassified over the years. However, as I have already explained, paleontologists have recently come to understand that the Pliosaur and the Elasmosaur morphologies arose multiple times. This realization has allowed paleontologists to more accurately reconstruct Cryptoclidid relationships by focusing on subtle characters, such as the arrangement of bones in the skull, the unique shape of the pectoral girdle, and the unusual nature of the clavicle.



Three families are now recognized within Cryptoclidia: the basal Jurassic **Cryptoclididae**, the Cretaceous **Leptocleididae**, and **Polycotylidae**.

Cryptoclididae is named after *Cryptoclidus*, its **type genus**. The type genus is the genus that the description of the family is based on and named for. It was about 3 m long and is known from a large number of individuals from the Middle-Jurassic of England. These Plesiosaurs are quite common, and enough individuals have been found that we know what they would have looked like throughout their development, from very young individuals to very old ones. This makes *Cryptoclidus* one of the best-studied and understood Plesiosaurs. If you have seen a plesiosaurus skeleton in a museum, there was a good chance it was *Cryptoclidus*.

The Cretaceous members of the Cryptoclidia come from two families that can be found all over the World: Leptocleididae and Polycotylidae. Both families looked like Pliosauroids, because they had large heads and short necks. However, when you look closely, their skulls show they are not true Pliosaurids.

First off, they have distinctive crests. Additionally, their lower jaws were very long and slender, supporting narrow teeth, and the joint between the two-halves of the jaw is long. Pliosaurids had a short joint between the two-halves of their lower jaws and more robust teeth.

Both families also had a triangular arrangement of bones in the roof of their mouth. They are common to all Cryptoclids. *Leptocleidus* and Polycotylids are also smaller than Pliosaurids. Fossils of fully-grown specimens are usually < 3 m long. An Australian Leptocleidid, *Umoonasaurus demoscyllus*, received a great deal of attention upon its discovery in 2006 due to its unusual mode of preservation. During fossilization, the bone was replaced with opal.

1.4 Results Of Morphological Differentiation

You have just learned about many different groups of Sauropterygians. You may have noticed, that throughout their evolution, these animals became more and more morphologically disparate. Their basal members were generally long, slender, lizard-like animals. The derived members, on the other hand, came in a variety of shapes and sizes.

What does this pattern of morphological differentiation say about the roles they played in their environments over time?

A. Regardless of their shape, derived Sauropterygians lived in shallow waters, and ate small Fish, like the basal members

B. Even though they were morphologically diverse, all derived Sauropterygians were big, and therefore ate other marine Reptiles

C. As Sauropterygians became more morphologically diverse, their behaviors and diets also became diverse

D. Like the strange and diverse animals found in the deep Oceans today, the extreme morphologies of the derived Sauropterygians were only suited to deep Oceans

A general trend in biology is that behavior follows morphology. Therefore, animals that looked different will generally have different behaviors. The derived Sauropterygians looked very different from each other and also from their basal ancestors. It is safe to assume that these animals have behaviors and lifestyles as diverse and different as their looks. Therefore, **C** is correct.

A and B are both incorrect because they indicate that the derived Sauropterygians all shared the same lifestyle. In addition, there may be some strange creatures alive at the bottom of the Oceans today, but equally strange things live near the surface.

These deep-sea creatures are all primary marine animals. They do not need to breathe air like Tetrapods. Therefore, D is also incorrect.

2 Plesiosaur Paleobiology

In the quest to solve the aquatic problem, Plesiosaurs raise the art of paleontological guesswork to new heights. Even with so much Fossil material, there is still great debate raging on how they use their four flippers for propulsion, how they hunted, how they mated, and whether they cared for their young. As we move into this next section of the lesson, we will focus on gathering the clues as to how Plesiosaurs solved the aquatic problem.

2.1 Locomotion

Let us start this section by talking about locomotion. There are many ways to move through the water. Most modern marine vertebrates, including Fish, Sharks, Sea snakes, and Crocodilians, use axial locomotion to generate thrust. Even Ichthyosaurs, which had four flippers, still generated thrust using a vertical caudal fin.

Plesiosaurs were almost unique to the animal kingdom in that they probably used their four large powerful flippers to generate thrust. They were not axial swimmers, because their short stubby tails are not effective for propulsion. Their Gastralia and ribs also caused them to have rigid bodies, and that would prohibit any sort of undulatory motion, meaning the Plesiosaur body would have remained absolutely stiff while swimming. No axial locomotion here, they would have been purely appendicular swimmers.

However, unlike most other appendicular swimmers, they have four well-developed flippers to generate thrust, not just two. Their body plan is unique among all living and dead organisms. Even Sea turtles, which also have four flippers, are significantly different, because their front and back flippers are different in size, and it is the front ones that generate most of the trust. Of course, this creates a problem: when paleontologists try to figure out how a long extinct animal moved, they usually look at a modern analogue.

What is a modern analogue?

It is the assumption that if an extinct animal has a similar skeleton to a modern animal, they probably moved in a similar way. One of the main reasons the Plesiosaur locomotion problem is so difficult is because we have no modern analogues. If we cannot say how they swam, it is very difficult to speculate on how Plesiosaurs would breed, hunt, or migrate. This makes a complete picture of Plesiosaur life in the Mesozoic Oceans even harder to reconstruct.

In this section, we will be discussing some of the clues that paleontologists have gathered to try to solve the problem of their locomotion, and we will outline some of the leading hypotheses that have resulted from this research.

2.1.1 Plesiosaur Locomotion Hypotheses

The Plesiosaur locomotion debate boils down to one question:

How did they move their flippers?

2.1.1.1 Hypothesis # 1: Underwater Flying

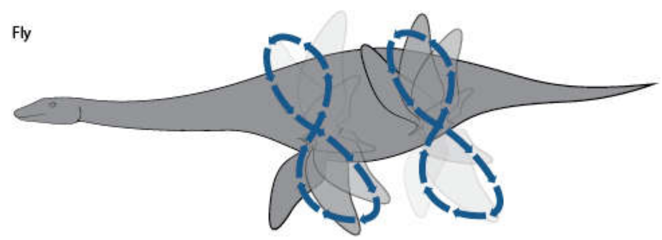


Illustration 92: 'Underwater flying'

There are three main hypotheses. The first is **underwater flying**. Think of the way a bird moves its wings, or the way a Penguin or a Sea turtle moves its flippers underwater. It is kind of a sideways figure eight motion.

2.1.1.2 Hypothesis # 2: Rowing

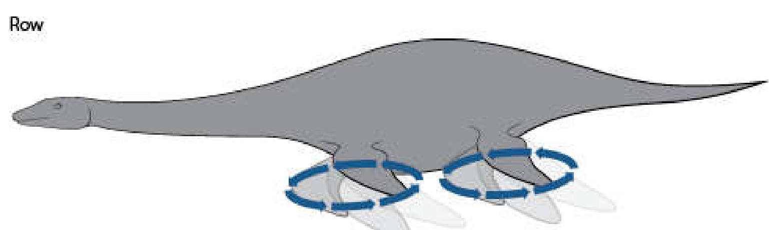


Illustration 93: Rowing

The second hypothesis is **rowing**, just like rowing a boat. The flipper pulls back horizontally with its wide edge to generate maximum thrust, and then the flipper moves forwards to its starting position, thin edge first to minimize drag. Modern Seals can do a similar motion with their flippers and so do we when we do breaststroke in the pool.

2.1.1.3 Hypothesis # 3: Paddling

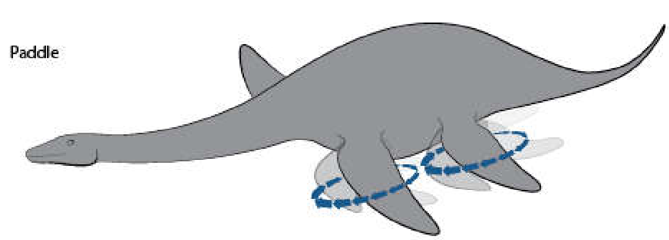


Illustration 94: Paddling

The third hypothesis is **paddling**, where the feet of the animal pulling through the water in a vertical plane. This is the way ducks swam, canoeists were paddling, and humans do freestyle. Sea lions also paddle using a belly slapping motion to move them forward.

2.1.1.3.1 A Swimming Dog

How does a swimming dog achieve thrust?

- **A.** Underwater flying
- **B.** Rowing
- **C.** Paddling

The dog is generating thrust by pulling its feet through the water in a vertical plane. Therefore, the correct answer is **C**, paddling. That is why this motion is called a **doggy paddle**.

Before we investigate the skeletal evidence, imagine a Plesiosaur swimming.

What mode of swimming do you picture? Do you imagine it using its flippers like wings to fly through the water? You imagine it rowing, and using its flippers like a two man rowboat? Alternatively, do you imagine the flippers moving down through the water like the paddles of a canoe?

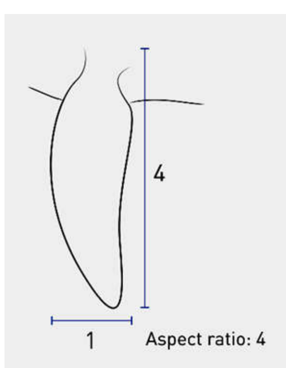
Regardless of what swimming style you picture, there are paleontologists who share your point of view. However, one of these hypotheses has gained far more support than the other two. However, we are not going to reveal which one just yet. Instead, clues will be provided as we discuss other aspects of their locomotion. By the end of our discussion, you should be able to combine the evidence, and make a more informed guess on how Plesiosaurs probably swam.

2.1.2 Plesiosaur Bodies

Let us start by looking at the body of the Plesiosaur. Plesiosaurs were well-adapted to minimize drag. They had smooth skin that was similar to the skin on the Porpoise or Ichthyosaur, and lowered viscous drag. The body shape of Plesiosaurs was also extremely streamlined to minimize inertial drag. They were roughly almond-shaped, 5.5 times as long as they were wide. This is the same specific body proportion seen in Sea lions, Penguins, and some swimming Birds, including Grebes and Cormorants. The elongated necks of Elasmosauromorphs would have caused additional issues regarding inertial drag, but we will discuss those a little later.

Paddling and flying motions both have a power stroke component from a down and back motion, whereas the rowing motion essentially moves directly backwards without much downward movement. Muscle attachment sites indicate that the muscles use to pull the limbs down and back were huge and powerful. The range of motion of the shoulder and hip sockets also supports the movements suggested by the muscles. They show that Plesiosaur flippers could move downwards below their bodies easily, had a limited range of motion front and back, and could not have moved their flippers upwards and behind their backs. This provides evidence against the rowing model, which requires a large amount of forward backward motion. The anatomy best supports the flying model as it uses the most up and down motion. However, the flying model does require some upward motion from the flippers, which would have been restricted by the Plesiosaur shoulder sockets.

Another interesting clue is that a rigid body seems necessary for flyers. Sea turtles and Birds both use flying motions, and their bodies are held rigid either by a plastron, or by an enormous sternum. Both of these structures provide a large bony plate down the front of the animal, which prevents any bending. Plesiosaurs also have very rigid bodies caused by their ribs and gastralia. This does not mean that the Plesiosaurs could not have paddled or rowed, but they do possess one of the necessary features for a flyer.



Now that we know that the body was stiff and attached to a massive swimming muscles, let us look at the flippers those muscles were attached to. Dividing a flipper's length by its width yields a measurement known as the **aspect ratio**. Therefore, a flipper 4 feet long and 1 foot wide has an aspect ratio of four. The aspect ratio can tell you a lot about how maneuverable an animal was, how much energy it expended to move, and whether it was built for fast acceleration or covering long distances.

Let us use airplanes as an example. Transport planes and most commercial planes have long thin wings. Long length, small width equals a high aspect ratio. These planes are built for long distance cruising since they generate more lift. However, the longer surface also generates more drag, making it harder for those planes to turn. Fighter jets have short broad wings, and therefore, a small aspect ratio. They are built for maneuverability; they can turn quickly since there is very little drag on their small wings. However, they require more energy to stay aloft for a long time since their short wings generate less lift.

2.1.3 Plesiosaur Flippers

2.1.3.1 Flipper Shape

Elasmosauromorphs and Pliosauromorphs generally differed in their flipper shapes. The Elasmosaurs had long, thin flippers, and the Pliosaurs had bigger, shorter flippers relative to their bodies.

Based on what you just learned about aspect ratios: Which of the two body forms has high aspect ratio flippers, and which has low aspect ratio flippers?

From this you should be able to tell which form was more suited for long distance cruising, and which was better for maneuvering and fast attacks.

Let us figure out the aspect ratio first. The Elasmosauromorph flippers were long, divided by a small width; this equals a large aspect ratio. The Pliosauromorph flippers were short, divided by a large width, which equals a small aspect ratio. Large aspect ratios, like those on cargo planes, are efficient at traveling long distances, but they are not very agile. Small aspect ratios, like those on fighter jets, are very fast and maneuverable, but require a lot of energy. Therefore, the correct answer here is that the Elasmosauromorph has high aspect ratio flippers better suited for long distance cruising, while the Pliosauromorph has low aspect ratio flippers, better at fast maneuvering.

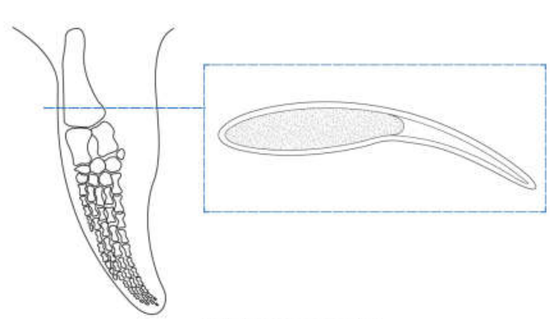
In Plesiosaurs, flippers with different aspect ratios evolved separately, and the animals had to develop attack strategies to match their physical abilities. A highly maneuverable Pliosaur would be much more suited to chasing prey as it darted through the water. Elasmosaurs were less maneuverable and would likely have had to rely on swimming long distances in search of situations, where they could ambush their prey who were spread out across the large expanse of the Ocean.

2.1.3.2 Flipper Structure

The flippers of Plesiosaurs contain large numbers of bones. Humans have only 2 or 3 phalanges per digit, but Plesiosaurs had as many as 18. In the animal kingdom, only Ichthyosaurs had a greater degree of hyperphalangy than the Plesiosaurs. These bones would have been fixed in strong connective tissue and cartilage, which is why we often find articulated Plesiosaur flippers. Because they really could not bend their elbows or wrists, Plesiosaur flippers were quite stiff, and a stiff flipper causes changes in direction by lifting or dropping the leading edge, like in a Bird's wing or a Shark's fin.

While traveling at high speeds, the back limbs of Plesiosaurs would probably have preformed most of the steering, leaving the front limbs free to generate maximum thrust. At slow speeds, it is likely that all four limbs would have generated thrust with minimum energy expenditure.

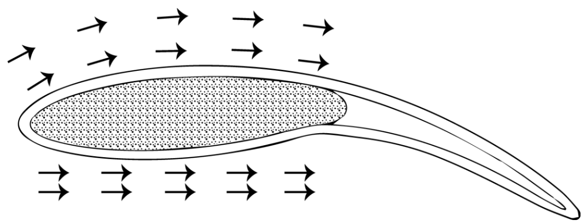
2.1.3.2.1 Hydrofoil Shape



Hydrofoil flipper cross-section

The stiff flipper also helped to maintain a **hydrofoil** shape. A hydrofoil is a very specific cross sectional shape. If you chopped off the pointed tip of a Plesiosaur flipper and looked at the cross section, you would see that the bottom of the flipper is flat and the top is rounded with a tapering back edge. This is the same cross sectional shape that you would see in a Bird's wing, or an airplane wing. In wings, however, we would call them airfoils, not hydrofoil, because they are used in air. The shape is optimal for generating lift, the force that pulls an object up.

Now how does that work?



As the water moves over the rounded top surface, it covers a greater distance than the water moving over the straight bottom surface. This means that the water molecules on top get more spread out. By spreading out, the molecules on top create empty space, which then sucks the animal up in an attempt to fill that empty space. This is the same way a vacuum works. This upward suction is what generates lift and keeps the animal moving in the direction they want to go. If you change the direction your hydrofoil faces, you can control the direction of the lift force that will pull you in.

The hydrofoil shape of the flippers is a major clue to locomotion. It provides some of the strongest evidence for one of the three locomotion types.

Based on what you just learned about how hydrofoils work: Which mode of locomotion does it provide for the most support?

A. Underwater flying

B. Rowing

C. Paddling

Hydrofoils almost certainly mean underwater flight, since lift is not generated with paddling or rowing. Therefore, **A** is the correct answer.

2.1.4 Plesiosaur Necks

Lets now look at the most recognizable feature of some Plesiosaurs, the long necks of the elasmosauromorphs.

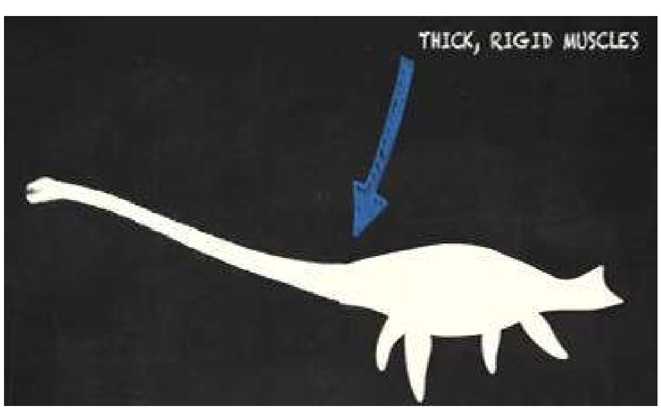
Based on what you learned about the mechanics of swimming so far in this lesson and the lessons before: Which position is the most likely for the long necks of a Elasmosauromorphs?

A. Upright

B. Coiled and Snake-like

C. Horizontal

Early paleontologists drew Elasmosaurs with the necks upright in an s-shaped curve or coiled like a Snake. These are common misconceptions propagated in popular media and are not the correct answer. Today we recognize that the vertebral shape, neck muscles, and neck weight would have limited lifting, bending, and coiling of the neck. Elasmosaurs swam horizontally with their necks stretched out in front. Therefore, the correct answer is **C**, horizontal. This position also would have been the most streamlined.



A Plesiosaur's long neck was likely a steering problem, as any movement would have caused deviation from a straight line as the animal swam through the water. Imagine having two steering wheels, one at the front and another at the back of a boat. As you try to steer, it would require a lot of corrections to keep going straight. To combat this problem, and also to avoid breaking their necks, Elasmosaurs had thick, rigid muscles at the base of their neck, which would have prevented any excessive movement.

These issues actually make the rowing and paddling hypothesis less likely. Both of these motions require a recovery stroke. This means that thrust is not generated continuously. As the animal accelerated and decelerated with each stroke, the stiff neck would have been jerked around causing changes in the animal's direction. Underwater flying generates thrust continuously during the entire stroke, allowing constant course correction and making this swimming style more likely, especially for the Elasmosauromorphs.

Another interesting adaptation of a long Plesiosaur neck was it had a slight curve. This curve would have generated a small amount of lift and stopped their heavy necks from dipping and continuously steering them downward.

2.1.5 The Most Likely Swimming Stroke

Now that we know more about Plesiosaur anatomy as it relates to locomotion, let us go back to the problem we introduced earlier in this lesson.

How did they actually propel themselves through the water using four giant flippers? Did they paddle like a four footed duck? Did they row like a two man Olympic rowing team? Or did they fly underwater like a penguin? Let us review our clues:

- Muscles: The power stroke would have come from a downwards and backwards motion, which is seen in both paddling and flying styles. Conversely, the rowing motion essentially moves directly backwards without much downward movement.
- Range of motion in shoulder and hip sockets: The sockets of the shoulder and hip also prohibit a rowing motion. The range of motion best supports the down and back movement of underwater flying, but the upward recovery stroke would have been restricted.
- Rigid body: The Gastralia give Plesiosaurs a rigid thorax, which is a necessary feature for a flyer, and is seen today in underwater fliers like Turtles and Birds.
- Cross-sectional shape of flippers: Plesiosaur flippers are efficient hydrofoils, able to create lift for flying underwater.
- Long neck: The long neck would have affected steering meaning, for Elasmosaurs at least, they would have benefited from a continuous motion of underwater flying.

Based on the evidence we have put together, let us rank the three modes of locomotion from least to the most likely.

2.1.5.1 Rowing

Thrust comes from the backstroke requires a recovery stroke and provides discontinuous thrust.

The problem?

Plesiosaur limbs are not shaped like an efficient oar and are restricted in their horizontal movement, making this the least likely mode.

2.1.5.2 Paddling

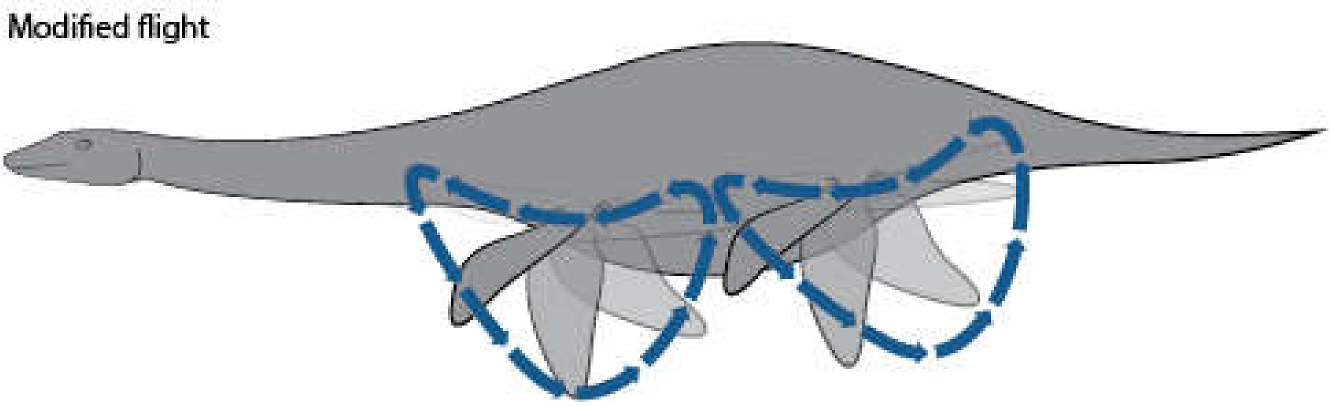
Thrust comes from the backstroke and requires a recovery stroke, where little thrust is generated.

The problem?

Plesiosaur limbs are not shaped like efficient paddles, but the required range of motion is possible making this the second most probable mode.

2.1.5.3 Flying

All four limbs would have moved primarily in the vertical plane with an axial figure eight rotational motion. This powerful motion provides constant thrust and keeps the animal moving more smoothly. In Plesiosaur limbs, the plane of moment is vertical, and the hydrofoil shape of the flippers is designed for flying. The only problem is that the limbs cannot be raised above and behind the animal's back, which restricts the recovery stroke. This is the most likely mode.



Together, these physiological clues provide the most support for the underwater flight model, but it is not perfect. It is more likely that Plesiosaurs used a modified swimming style that combined elements of flying and rowing. The down stroke, or power stroke, would provide lift and thrust as in flying, but the recovery stroke was probably more similar to the horizontal recovery of the rowing style. It is probable that Plesiosaur flippers would have moved in near synchronization, with the front and back flippers moving almost at the same time resulting in maximum thrust and minimum drag. All four flippers would have been used as propulsive elements, with the front limbs generating most of the thrust and the back flippers generating some thrust and the majority of the steering. This would result in more speed, acceleration, and maneuverability. Since it is energetically costly to use constantly all four flippers, it is possible that Plesiosaurs would have glided between strokes, or used only the front flippers at low cruising speeds.

2.2 Feeding

The modifications for locomotion that we just discussed would have impacted the lifestyles of the long-necked Elasmosauromorphs and the large-headed Pliosauromorphs. Recall that these two body forms evolved multiple times in the Plesiosaur lineage and each form probably had different lifestyles.

Which morphotype do you think was specialized for which feeding behaviors?

A. Both morphotypes ambushed small prey

B. Both morphotypes chased down large prey

C. Elasmosauromorphs ambushed small prey and Pliosauromorphs chased down large prey

D. Pliosauromorphs ambushed small prey and Elasmosauromorphs chased down large prey

Elasmosauromorphs, with their pointy teeth and long necks, were most likely Fish eaters. The long neck allowed them to snap up their prey without having to chase them. The small heads and thin necks would have prohibited them from eating large prey. Pliosauromorphs, with their short necks and large flippers, had high-speed agility and the ability to dive. They chased down their prey and would have used their large, powerful jaws to dismember it. Therefore, the correct answer is **C**.

2.2.1 Elasmosauromorph Feeding

The Elasmosauromorphs with their long necks and their high aspect ratio flippers were specialized for long distance cruising. Their fine pointed, recurved teeth were used to catch and hold on to small slippery prey. As we discussed earlier, it is now accepted that the long-neck plesiosaurus almost certainly swam with their necks stretched out in front of them. Fish and Cephalopods might not have recognized the relatively small heads as much of a danger. Since the large, threatening bodies would have been much further away.

Fossilized remains of Plesiosaurus stomach contents show that their most common prey items were Fish and soft-bodied Cephalopods. However, other small prey items have been found including small Pterosaurs, and even an Ichthyosaur embryo.

2.2.2 Pliosauromorph Feeding

The short-necked Pliosauromorphs are thought to have been diving hunters. Like modern Sperm whales, they would have been the predominant marine predators of their time. Their flippers, which could be as long as 2 m, had a low aspect ratio, specialized for power, maneuverability, and prodigious speed. The bigger flippers also provided the downward acceleration needed to dive. Their massive, stubby, conical teeth are characteristic of Cephalopod feeders, but would have also been efficient at dismembering large prey by shaking and twisting them.

This diving lifestyle is supported by the presence of avascular necrosis in their limb bones. This suggests that they suffered from decompression syndrome, also known as the bends. Fossilized stomach contents show that they were likely opportunistic hunters, eating mostly Fish and Cephalopods, but Sharks, Ichthyosaurs, and other Plesiosaurs are also found in their stomachs. Even Dinosaur bones have been found in the stomachs of Pliosaurs. This was likely from a floating carcass; since Pliosaurs almost certainly would not have hunted land bound Dinosaurs.

2.2.3 Gastroliths

Illustration 95: *Plesiosaur* Gastroliths

One thing found in the stomachs of all types of Plesiosaurs, regardless of what they ate, is Gastroliths, sometimes-called gizzard stones.

Plesiosaur fossils are very often found associated with a mass of these small, smooth stones in their abdominal region. Why would Plesiosaurs swallow them?

A. Their bodies needed the minerals found in the rocks

B. They ate the rocks when they could not find real food

C. They needed them to aid in the digestion of their prey

D. They accidentally swallowed them when they ate prey off the Ocean bottom

Today Gastroliths can be found in the stomachs of Lizards, Fish, Crocodilians, Turtles, Snakes, Mammals, and Birds, where they help break apart large pieces of food that the animals swallow. Therefore, the correct answer is **C**.

The minerals an animal needs to survive are usually obtained from its food. The animal would not eat rocks if they were hungry, as they would not make the animal less hungry. Finally, the Gastroliths are too large to have been accidentally swallowed. Therefore, A, B, and D are not correct.

Some scientists think the stones may also have acted as ballast and helped achieve neutral buoyancy. Some paleontologists have guessed that the Plesiosaurs actively swallowed stones or regurgitated them depending on whether they wanted to float or sink. However, with a 5 – 6 m long neck, it was probably very difficult to regurgitate stones, and in the open Ocean it would be hard to find the appropriate rocks every time they wanted to dive. It seems unlikely that they were using them to control buoyancy actively, and therefore, they were probably digestive aids only.

2.2.4 Senses: Hunting Underwater

Since all Plesiosaurs were active predators, they must have had highly developed sensory systems in order to locate their prey items. Like the Ichthyopterygians, they had bony rings inside their large eyes. Possible functions include supporting the eyeball under the pressure of deep water, and facilitating quick changes in focus and aperture, just like using the focus knob on binoculars. This adaptation would have made them extremely effective visual predators in dark or murky water.

Plesiosaurs, like many aquatic animals, possessed no eardrum, which is an adaptation to hearing airborne sounds. Aquatic animals hear by direct transmission of the vibrations to their inner ear through their skull, and therefore, do not require the specially adapted eardrum.

Smelling under water might have been facilitated by scoop shaped openings in the roof of their mouth that directed water into channels where scent receptors were located, and then out through the external nostrils. This arrangement might have enabled a sense of smell allowing them to hunt by smell, like a Shark.

2.3 Reproduction And Sociality

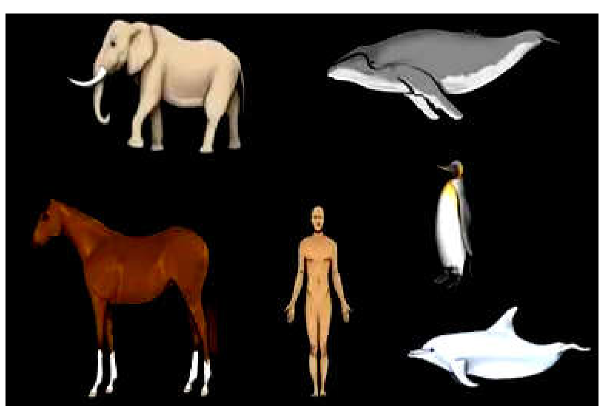
Reproduction and sociality are harder to understand than locomotion and feeding, because they do not leave direct skeletal evidence. For a long time, paleontologists have debated whether Sauropterygians were oviparous, meaning they laid eggs, or viviparous, and gave live birth. Many paleontologists thought that like modern Sea turtles, Plesiosaurs might have come ashore to lay their eggs. However, with enormous flippers, a massive body, and, in some cases, an extremely long neck or oversized head, they would have been extremely awkward out of the water and very vulnerable to predators. In fact, both Pliosauromorphs and Elasmosauromorphs had such massive heads and necks, that they could not even have lifted them out of the water. It is extremely unlikely that Plesiosaurs ever left the water, but, without solid proof, the egg-laying hypothesis persisted.

Other paleontologists thought that like Ichthyosaurs, Plesiosaurs gave birth to live young underwater. If they did, it would mean that these animals would be freed from ever having to go onto land. However, for a long time, no evidence of viviparity was found. Now, thanks to the recent discovery of three remarkable specimens, we know that both basal and derived Sauropterygians were viviparous. Two pregnant specimens of a Pachypleurosaur, *Keichosaurus*, were found with embryos in the abdominal cavities, indicating that basal Sauropterygians gave live birth.

Illustration 96: *Polycotylus* giving birth (Live restoration)

A subsequent discovery of a pregnant Plesiosaur Fossil, from Kansas in 2010, show that derived Plesiosaurs also gave birth to live young. The impressive specimen is a 5 m long *Polycotylus* mother with a single 1.5 m long fetus inside her abdomen. This is unusual, as all other Mesozoic marine Reptiles had several babies. The Plesiosaurs appear to have gestated only one big baby at a time.

Here are some examples of modern animals that generally give birth to a single live offspring.



What features do they have in common?

Choose all that apply.

A. They live in social groups based on extended families

B. They are predators

C. Offspring are provided with a lot of parental care

D. They mate for life

Not all of these examples are predators. Baleen whales, for instance, are filter feeders; therefore, B is not correct. Only some Whales, Penguins, and Humans mate for life; therefore, D is not correct. However, all these animals that give birth to a single large baby tend to provide them with a lot of parental care. They also commonly live in social groups based on extended families. This evidence suggests that Plesiosaurs may have cared for their young, and that they could have lived in pods like modern Dolphins. There has been no direct evidence of parental care or social living, but it is an interesting idea. The correct answers here are **A** and **C**.

A juvenile Plesiosaur recovered from South Dakota provides additional indirect evidence for parental care in Plesiosaurs. Cretaceous South Dakota was very far from shore. It would have been dangerous for a small predator to be in the open Ocean on its own. Therefore, it is possible, that a parent would have accompanied the juvenile.

Further inferred evidence for reproductive behavior can be found in South Australia, which is a great place to go if you are looking for baby Plesiosaurs. Interestingly, there are a high proportion of juveniles found here, more than anywhere else in the World. This great number of babies suggests that South Australia could have been a breeding ground, where pregnant mothers would have gathered to give birth. They may have been attracted to these waters because of high concentrations of Plankton, Fish, and Squid.

2.4 Paleobiology Conclusion

As you have seen, Plesiosaurs were uniquely evolved to overcome the aquatic problem. They did not evolve the more commonly used axial locomotion, but retained the locomotive capabilities of all four limbs. There is considerable debate over how these limbs functioned, but most paleontologists support the idea of modified underwater flight. The maneuverability of the Elasmosauromorphs would have been affected by the aspect ration of their flippers, and also by their long neck, likely resulting in an ambush strategy targeting small Fish. Pliosauromorphs, freed from the constraints associated with the long neck, were able to actively pursue and consume larger prey. Like the Ichthyopterygians, the Sauropterygians developed viviparity early in their evolutionary history, but likely invested a higher degree of parental care into fewer offspring.

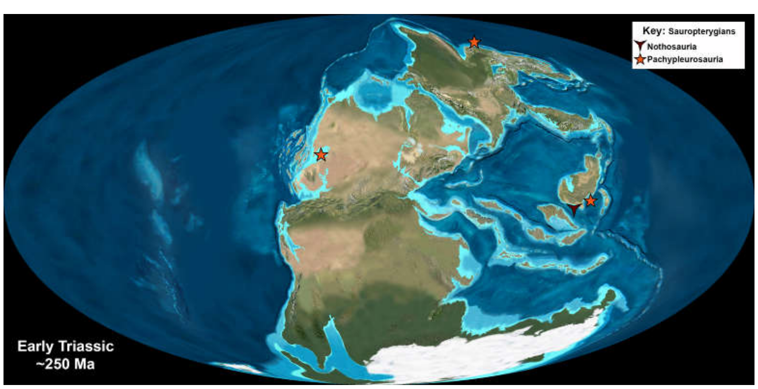
The second major group of marine Reptiles solves the aquatic problem in a completely unique way, which has not been replicated by any modern animals. Still, some elements of their anatomy and behavior converge upon solutions we have seen in other groups. Clearly, though unique, their adaptations ended up being highly successful, resulting in a 180,000,000 y reign, which was the longest of any of the predatory marine Reptiles.

3 Sauropterygian Distribution Through Space And Time

To some extent, the patterns of Sauropterygian evolution and distribution closely resemble those of the Ichthyopterygians that we explored last lesson. These groups shared the seas during the first 150,000,000 y of Sauropterygian evolution, before the Ichthyopterygians went extinct during the Mid-Cretaceous. Sauropterygians originated and diversified during the Early-Triassic. The near-shore forms went extinct by the end of the Triassic. Fully aquatic forms dominated during the Jurassic, and a small number of derived taxa hunted the Cretaceous seaways until their extinction. Let us go back to our maps to explore the patterns of Sauropterygian distribution, and some famous Fossil localities.

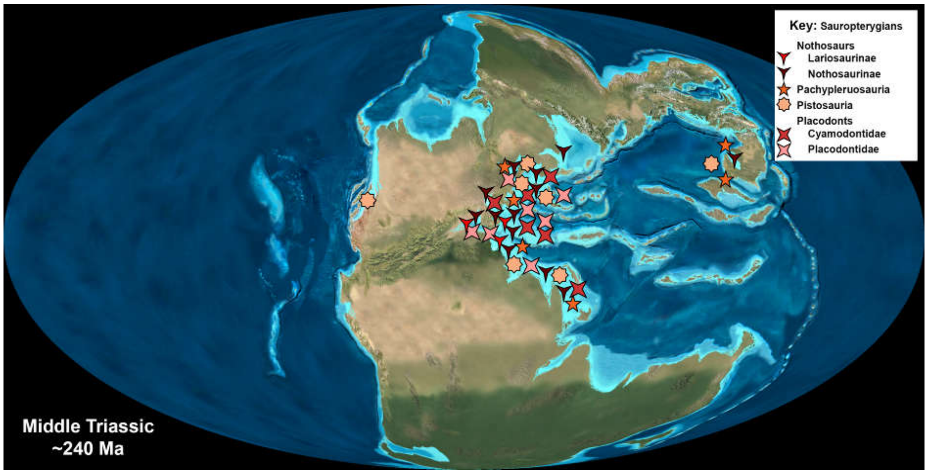
3.1 Triassic

3.1.1 Early-Triassic



The Sauropterygian story starts by the end of the Early-Triassic, in the shallow coastal waters of the Tethys. Their development appears to have been closely tied to global sea level rise and the resulting continental flooding during the Triassic. The abundance of separate marine basins favored **endemism**, or the evolution of unique species in different localities.

3.1.2 Mid-Triassic



Placodonts, *Nothosaurus*, Pachypleurosaurs, and Pistosaurs all inhabited the same shallow seaways during the Mid-Triassic, at the time when the first Dinosaurs evolved on land. This variety of similar looking basal Sauropterygians managed to live at the same time without directly competing with each other, and this was probably accomplished by endemism and **niche partitioning**. The animals would either have to live in slightly different places or would have had to specialize on different resources and niches within the same environment.

3.1.2.1 Lack Of Fossils In Older Rocks

By the Middle-Triassic, all of the basal Sauropterygian lineages were well-adapted to the aquatic environment and looked very distinct from each other. This means all the basal Sauropterygian lineages probably originated in the Early-Triassic, but for some reason, Fossil evidence of these groups from this time is rare.

Can you think of any reasons why their fossils are not found until stratigraphically younger rock layers? Check all that may apply.

A. Early-Triassic strata are rare or poorly explored

B. Early-Triassic Sauropterygians were likely small, and smaller animals do not fossilize as well

C. Early-Triassic Sauropterygians lived in a near-shore environment, which does not favor the preservation of articulated fossils

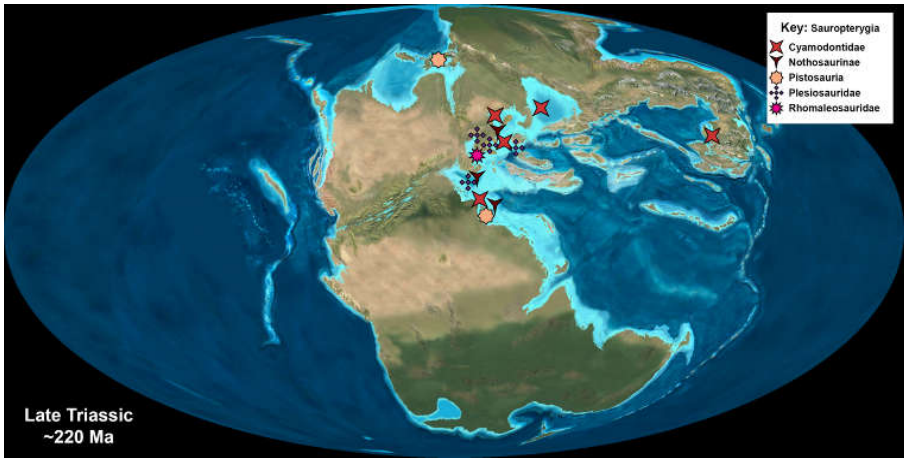
D. Early-Triassic Sauropterygians did not have bones and would not have fossilized easily

Nothosaurs, Pachypleurosaurs, Placodonts, and Pistosaurs are morphologically distinctive and diverse by the Middle-Triassic. Therefore, we assume that they evolved early, even if we have not yet found the fossils to support this. These groups are all vertebrates; therefore, they would have had bones that could have fossilized; therefore, D is incorrect.

However, the earliest Sauropterygians were small, with fragile bones that are less likely to be preserved. This is especially true in the turbulence of shallow water environments; therefore, **B** and **C** are correct.

The lack of fossils from the Early-Triassic could also represent a collection bias. The strata that were deposited at that time could have been eroded away by subsequent geological processes. Less of those strata could currently be exposed, or these strata may be unexplored. Any of these cases would lead to an artificially low number of known fossils from that time. Therefore, **A** is correct as well. Additionally the Early-Triassic is a much shorter time period than the Middle- or Late-Triassic. Therefore, less rock was deposited during this time.

3.1.3 Late-Triassic



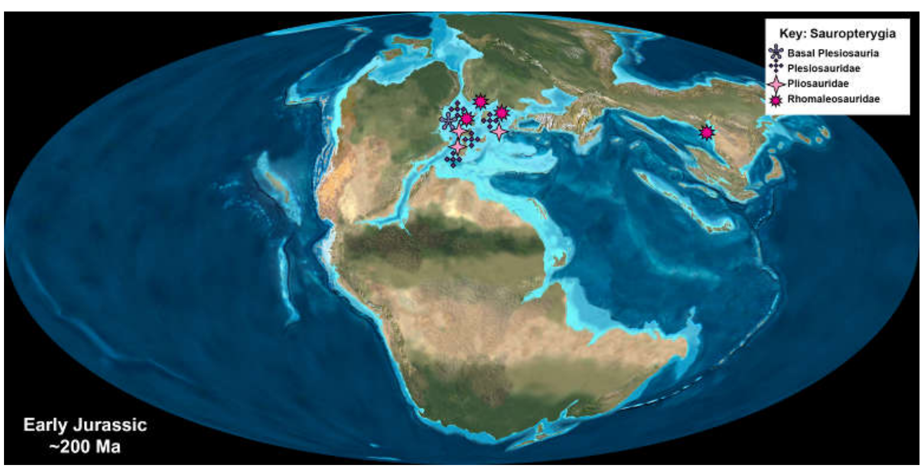
By the Middle-Triassic the first Placodonts had appeared around present day Israel. They diversified and spread around the Western-Tethys to the Germanic-Basin and the Alps. Pachypleurosaurs and *Nothosaurus* also became abundant around the Tethys and the Western region of the developing Pacific Ocean in what is Southeastern-China today.

The abundance of extinct reptile fossils has long been known in the Guizhou province of China, though for centuries they were considered to be petrified dragons and were symbols of good fortune. The Eastern-Pacific stretched to modern day Wyoming, and Pistosaurs are known from deposits from those basins as well as the Western-Tethys.

During the Middle-Triassic, all Sauropterygian groups were taxonomically diverse and morphologically disparate. However, an extinction event at the end of the Late-Triassic wiped out the Placodonts, *Nothosaurus*, and Pachypleurosaurs. Most Pistosaurs went extinct as well. The only group to survive was the Plesiosauria, which originated during the Late-Triassic. These Sauropterygians were larger and better adapted to living and feeding in the open Ocean. This likely helped them survive the sea level fluctuations at the end of the Triassic.

3.2 Jurassic

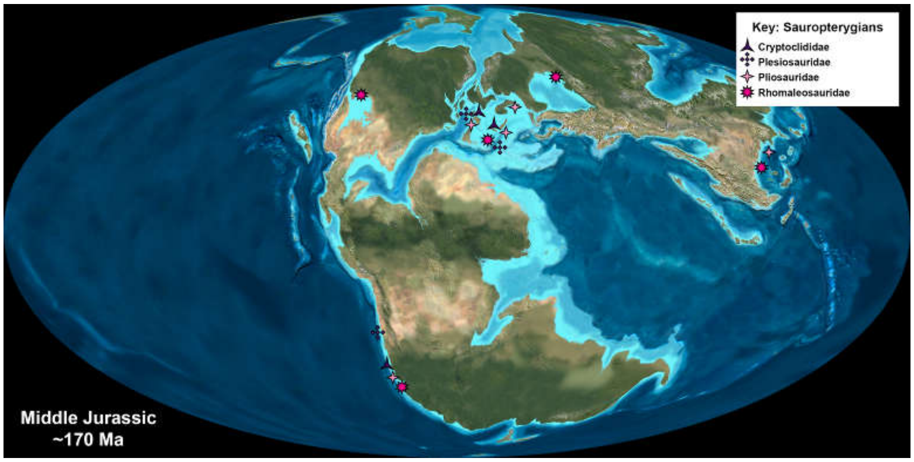
3.2.1 Early-Jurassic



By the beginning of the Jurassic the Sauropterygian family tree was pruned to a single lineage, the Plesiosaurs. Plesiosauria diversified dramatically during the Jurassic, from the basal *Archaeonectrus* and *Attenborosaurus*, which are found in the UK.

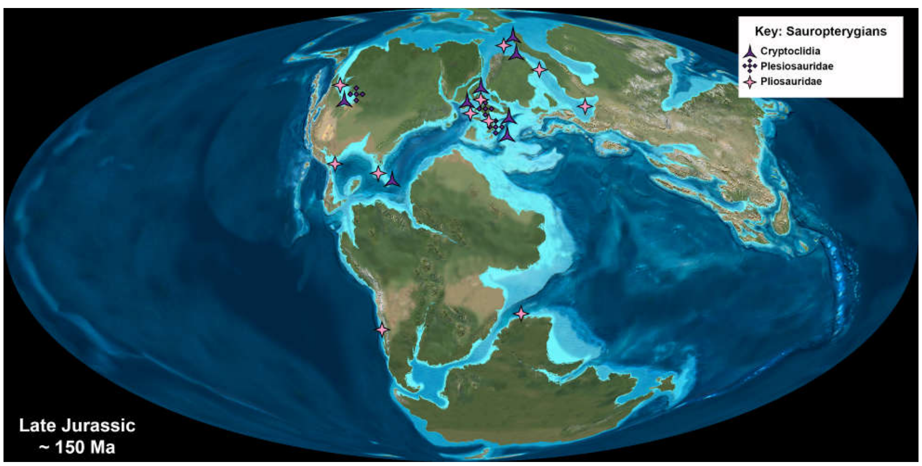
Plesiosaurus is also known from the UK, but is from a slightly younger deposit known as the Blue Lias, which is exposed in the sea cliffs of Lyme Regis, where Mary Anning made her discoveries. One of the most diverse and specialized clades of Plesiosaurs, from the Early-Jurassic, was the Rhomaleosauridae, which were the first Plesiosaurs to achieve a truly worldwide distribution.

3.2.2 Mid-Jurassic



By the Middle-Jurassic, the massive Pliosauridae had replaced Rhomaleosauridae as the top predators in the World's Oceans. Plesiosaur fossils are found in Australia, France, India, UK, and the US. Pliosaurs were not alone in the Middle-Jurassic seas, because the Cryptoclidids also diversified during this time. The Oxford- and Kimmeridge-Clays of the UK are Middle- and Late-Jurassic strata that were heavily mined for building materials. Miners unearthed a multitude of fossils of Dinosaurs, Thalattosuchians, and excellently preserved Plesiosaurs. These strata preserved abundant Cryptoclidids and Pliosaurid fossils such as *Cryptoclidus* and *Paleoneustes*.

3.2.3 Late Jurassic



During the Late-Jurassic, global sea level rise resulted in the formation of an interior seaway, the Sundance Sea, which bisected North America. The Sundance was home to two species of Cryptoclidids and one Pliosaurid.

Illustration 97: ***Tatenectes laramiensis*** **(Fossil)**

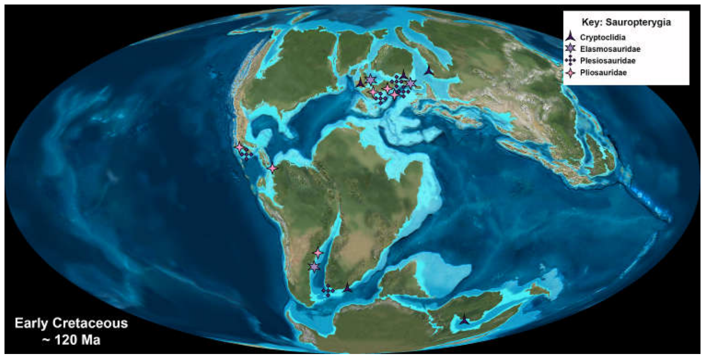
One Cryptoclidid, *Tatenectes laramiensis*, appears to have been particularly well-adapted to shallow water. Its body was wide and flat, kind of like a Sea turtle, which might have helped it to stay upright in strong currents.

The formation of the Sundance Sea is the first time in the history of Sauropterygians that the major sea way covered the continent of North America. Therefore, it makes sense that the first evidence of Canadian Sauropterygians can be found from the Late-Jurassic rocks. In fact, in 2008 a new species of Rhomaleosauridae called *Borealonectes* was discovered on one of the Arctic islands of Canada.

However, by the end of the Jurassic, erosion and tectonic uplift from the formation of the Rocky Mountains filled in the Sundance Basin, returning it to terrestrial habitats. Cryptoclidid Plesiosaurs went extinct by the End-Jurassic in the marine Tithonian extinction, though some species of Pliosauria survived into the Cretaceous.

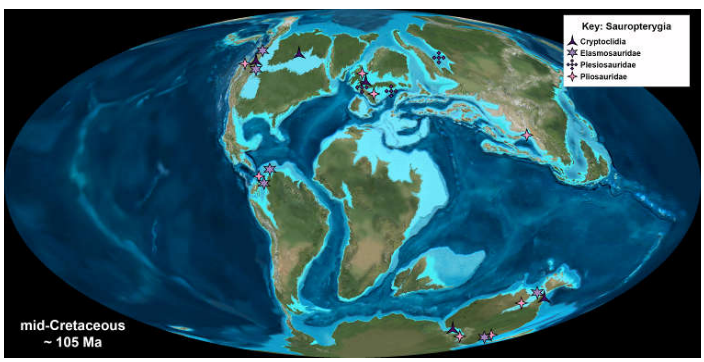
3.3 Cretaceous

3.3.1 Early-Cretaceous



Early-Cretaceous marine deposits are poorly known, but Plesiosaurs from this time are represented by species of Leptocleidids from Germany and the UK. The lack of marine reptile fossils from this time represents another case of collection bias.

3.3.2 Mid-Cretaceous



The Mid-Cretaceous saw the development and diversification of the extremely long-necked Elasmosaurids. The two earliest Elasmosaurid species are known from Columbia and Australia.

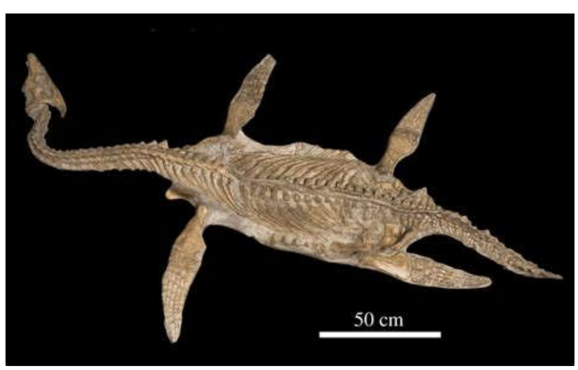
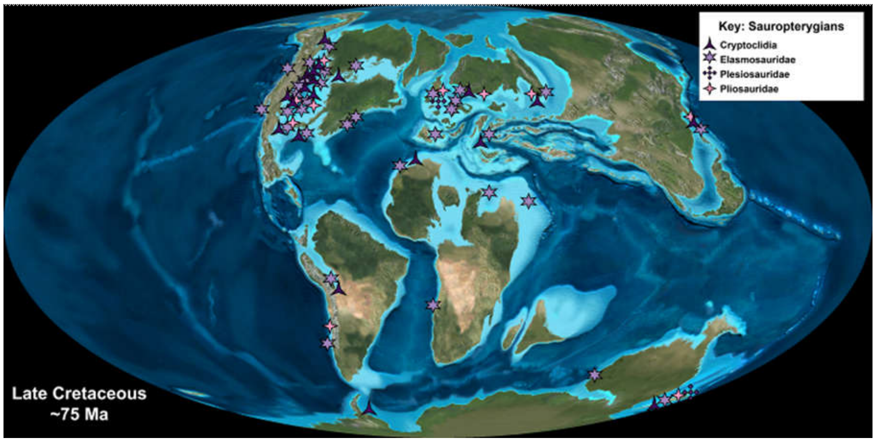


Illustration 98: *Nichollssaura borealis* (Fossil)

Leptocleidids, such as *Nichollssaura borealis* from Alberta, were largely replaced by Polycotylids during the Middle-Cretaceous.

3.3.3 Late-Cretaceous



One of the last Pliosaur mega-predators is *Brachauchenius*, who measured in at more than 11 m, and lived during the earliest part of the Late-Cretaceous. Even though it is one of only two Pliosaurids to survive into the Late-Cretaceous, these animals still went extinct long before the End-Cretaceous extinction event.

Sea level fluctuations during the Cretaceous caused the rise and fall of the Western interior sea many times. Inhabiting this sea were Polycotylids like the 3 m long *Trinacromerium*, who possessed the longest flippers ever known, equal in length to its torso. These long flippers allowed it to reach unprecedented speeds.

Polycotylids shared the sea with other record-holders, like the long-necked Elasmosaurids, such as *Elasmosaurus* from Kansas and *Albertonectes* from Alberta. Canadian Cretaceous Sauropterygians represent the community of the Northern half of the Western interior sea, which covered most of what is now Western Canada.

Illustration 99: *Albertonectes vanderveldi* (life restoration)

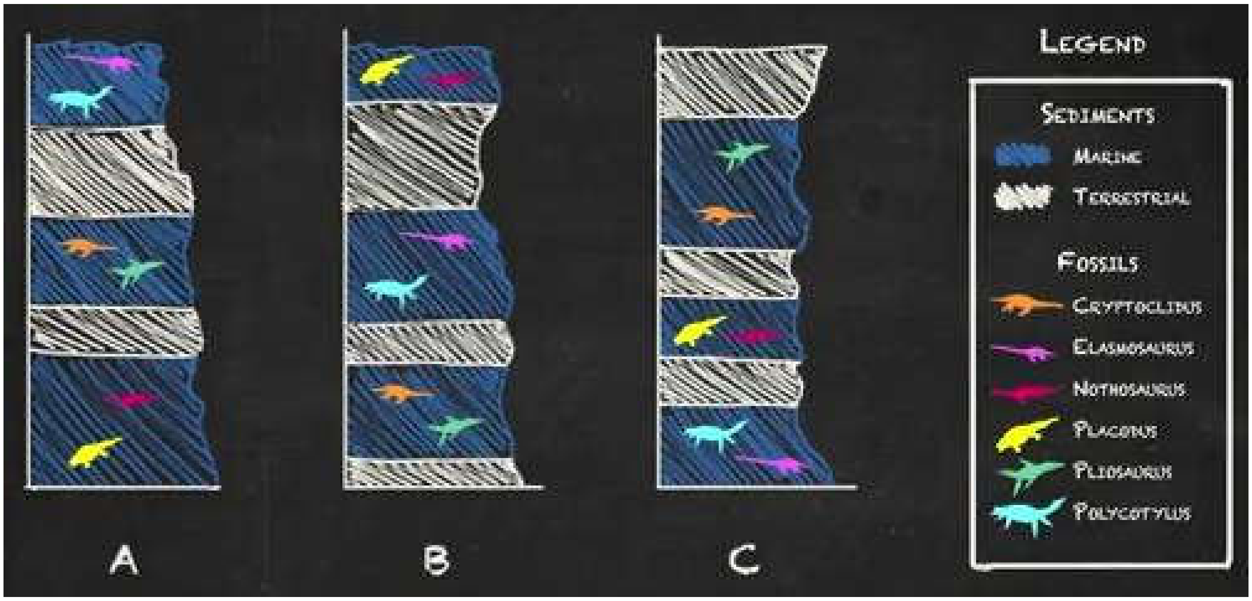
Multiple species of Elasmosaurid, Pliosaurid, and Polycotylid remains have been found in Late-Cretaceous strata from all of the Western Canadian provinces. These discoveries include the giant-flippered *Trinacromerium kirki* from Manitoba, and *Albertonectes vanderveldi* from Alberta, which has the most cervical vertebrae of any known elasmosaur. The abundance of Elasmosaur fossils from the Late-Cretaceous Canada reflects their diversity all around the globe. During this time, Elasmosaurs achieved worldwide distribution, and their fossils have been found on every continent, including Antarctica.

Interesting finds, like *Cimoliasaurus* from the Northwestern territories of Canada, tell us that Plesiosaurs almost certainly went extinct, due to the End-Cretaceous mass extinction event. *Cimoliasaurus* is found in rock layers that date from the very end of the Cretaceous. Therefore, we know that at least some lineages of Plesiosaurs lived up until this time.

3.3.3.1 Stratigraphic Columns

The Late-Cretaceous mass extinction caused the extinction of all Plesiosaurs, 66,000,000 y ago, and ending Sauropterygian dominance.

Based on what you know about the law of superposition and biostratigraphy, and what you have learned about the evolutionary history of Sauropterygia: Which of the following three stratigraphic columns correctly depicts how assemblages of Sauropterygian fossils might be found?



Think back to what you know about sedimentary rocks. The law of superposition states that in undisturbed sedimentary rocks, the younger layers are deposited later than the older layers and must be found above them. You have also learned when different groups of Sauropterygians lived. Therefore, you should have identified the stratigraphic column in which the most primitive Sauropterygians are found in the lowest marine layer.

Placodonts and *Nothosaurus* are basal Sauropterygians and are found in the oldest layers at the bottom. Cryptoclidids and Pliosaurids lived during the Jurassic, and Elasmosaurs and Polycotylids inhabited Cretaceous seaways at the top of the stratigraphic column. Therefore, stratigraphic column **A** is correct.

3.4 Conclusion

Sauropterygia was the longest-lived lineage of the extinct marine Reptiles. They showed a huge variety in form and function, from the durophagous Turtle-like Placodonts of the Triassic to the long-necked Fish-eating Elasmosaurs of the Late-Cretaceous. We now know that the two main body plans, seen in the derived Plesiosaurs, the Pliosauromorphs, and the Elasmosauromorphs evolved multiple times and do not necessarily indicate close relationships between species. Plesiosaurs were unusual among secondarily marine Tetrapods in that they did not rely on axial locomotion, but rather retained four functional limbs that they likely moved in a modified flight pattern. The Pliosauromorphs in particular likely used these hydrofoils to generate impressive speeds to pursue their prey.

Strong evidence has been found that Plesiosaurs gave birth to live young and likely invested a great deal of effort into raising a single offspring at a time. Plesiosaurs eventually colonized the World's Oceans, which they shared with the Ichthyopterygians for the first 150,000,000 y, and the Mosasauroids, which are the subject of the next lesson, for the last 30,000,000 y of their existence. Their fossils are found on every continent and likely inspired many myths and legends. The lives of these animals were no less wonderful than the stories they inspired.

I hope you enjoyed this lesson on Sauropterygians and their evolutionary journey. Let us move on to the final lesson, where we will be discussing the evolution, ecology and diversity of the Mosasauroids: the last major marine reptile group to rule the seas.

Mosasauroids

1 Mosasauroid Systematics

Illustration 100: Grand Animal de Maastricht

In 1808, Baron George Cuvier, who is known as the father of comparative Anatomy and Paleontology, described the fossilized jaws of an enormous reptile, which he called the **Grand Animal de Maastricht**. The fossilized jaws had been found deep in the mine in the Netherlands. They looked like the jaws of a modern monitor Lizard, but were > 1 m long.

At the time, fossils were not well understood. Extinction was not a well-accepted fact, and Darwin's **Origin of Species** would not be published for another 50 y. Naturalists at the time had no idea what to make of the unfamiliar fossils, classifying them as Fish, Whales, or Crocodiles. Cuvier was in the minority by classifying this Fossil as a Lizard. Although Cuvier was not the first to recognize the Lizard features of the skull, he was in a prominent enough position that his words carried great weight. At the time, he was an anatomist at the National Museum in Paris.

Illustration 101: *Mosausaurus Hoffmannii* (Fossil)

The Dutch Fossil would go on to become the first Mosasaur to be described, named for the Meuse River, or Mosa in Latin, where it was found. Cuvier's Fossil was an example of *Mosausaurus Hoffmannii*, which inhabited the World's Oceans about 70,000,000 y ago, well into the second half of the Cretaceous. While Tyrannosaurs ruled the land, Mosasaurs dominated the seas. At this point in time, near the End-Cretaceous, the Mosasaurs had been around for about 25,000,000 y. Their ancestors were small terrestrial Lizards that left the land for a life in the water about 95,000,000 y ago. Once in the water, the shore-dwelling Mosasaur ancestors began to evolve rapidly.

What is most remarkable about Mosasaurs is their leap to the top of the aquatic food chain. Within moments, geologically speaking, they went from small terrestrial Lizards to the apex predators of the Cretaceous seas. For comparison, Ichthyopterygians and Sauropterygians evolved for about 50,000,000 y before they could be considered dominant marine predators. Mosasauroids took only 10,000,000 y.

Their adaptations to solve the aquatic problem included the evolution of paddle-like flippers and the lengthening of their tails, which also developed the hypocercal tail fin. Recall that the hypocercal tail fin has one lobe that is more pronounced, or larger, than the other lobe. This is the type of tail fin we have seen in some Fish, Sharks, and Ichthyosaurs. These adaptations made them proficient at pursuing and ambushing their prey and allowed them to conquer the Oceans. During the 25,000,000 y that they prospered, the Mosasaurs spread from pole to pole, leaving their remains in North and South America, Europe, Africa, Australia, Antarctica, and Asia. This incredible group will be the last clade we investigate which is appropriate, since they were the last major marine Reptile group to evolve and represent the last time that Reptiles ruled the seas.

1.1 Mosasauroid Relationships To Other Diapsids

What exactly are Mosasaurs?

Mosasaurs are squamates, the group of Reptiles that includes all extent and Fossil Lizards and Snakes. The relationship of Mosasaurs among squamates is a subject of ongoing controversy, though most scientists agree they are closely related to anguimorph Lizards. Anguiomorphs evolved during the Jurassic and have survived into the present time, including modern forms such as the Gila monster, Komodo dragons, and numerous small Lizards.

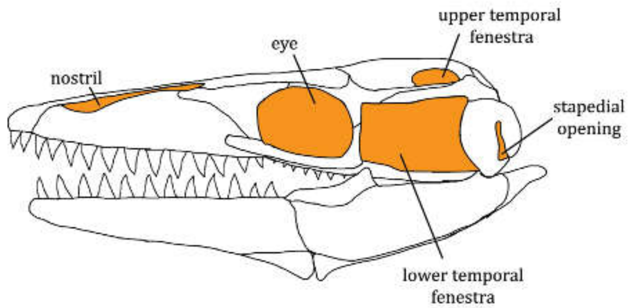


Illustration 102: Skull of *Tylosaurus* showing the two temporal fenestrae

All squamates, including Mosasauroids, have a lizard-like skull with two openings behind the orbit. Remember that the Diapsid condition, where the skull has two openings behind the orbit, also occurs in Crocodiles and Dinosaurs. All Mosasaurs also have an intramandibular joint located in the middle of each jaw. These lower jaws are loosely connected at the front of the mouth, forming the intramandibular joint. The flexibility of these two joints allowed Mosasaurs to open their mouths very wide, and gave them the ability to swallow large objects. This unique characteristic is also shared with Snakes and is one of the reasons that Snakes and Mosasauroids are thought to be sister groups.

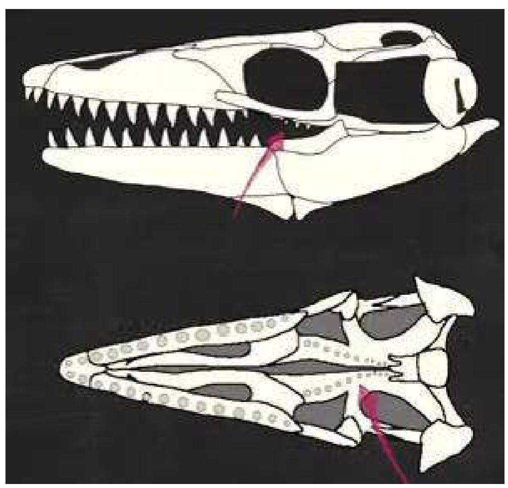


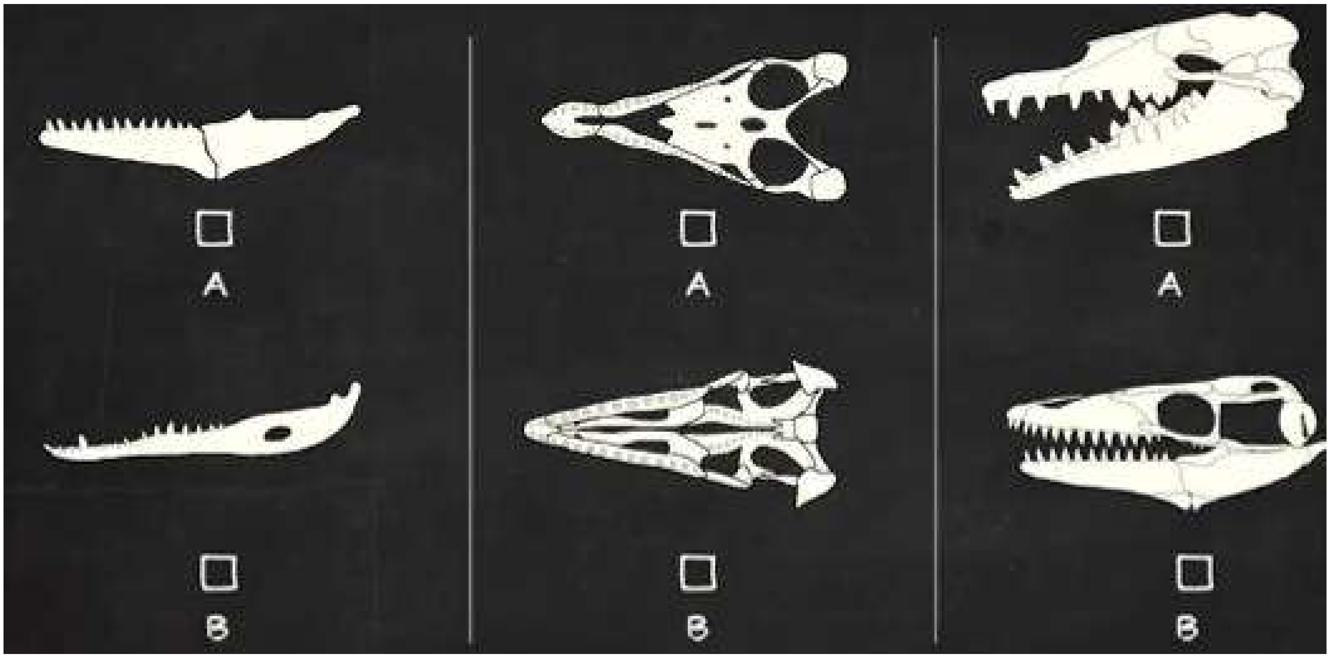
Illustration 103: Pterygoid teeth

Mosasaurs also have another special feeding adaptation. They had teeth on the pterygoid bones in the roof of their mouths, and these pterygoid teeth kept slippery prey from escaping the mouth while they were being swallowed, yet another feature that Mosasaurs share with Snakes. If this Snake-Mosasaur sister group hypothesis is accurate, then it is possible Snakes evolved from aquatic Lizards like the Mosasaurs did. These two lineages, the Snakes and the Mosasaurs, are often placed together with their common ancestors in the group of Lizards called the Pythonomorpha, which means snake-like.

As mentioned, many of the characteristics that make a Mosasaur a Mosasaur, including the Diapsid skulls, intramandibular joints, and pterygoid teeth are also common to Snakes. However, unlike Snakes, Mosasaurs have well developed aquatically adapted limbs that exhibit hyperphalangy and a much longer and more laterally compressed tail than is seen in Snakes. One particularly important bone when it comes to differentiating Mosasaurs a bone at the back of the skull called the quadrate. In life, it acted as a hinge that connected the lower jaw to the skull, and it also supported cartilaginous structures involved in hearing. The quadrate was robust, and therefore, is commonly preserved. This is fortunate, because variations in this bone help to identify different groups of Mosasaurs. Even a partial quadrate helps identify the genus of a fragmentary Mosasaur specimen.

1.1.1 Mosasaur Fossils

Were you able to recognize the diagnostic characters of Mosasaurs? Of the following sets of fossils, select which one comes from a Mosasaur.



Remember to look for the intramandibular joint as seen in jaw A, pterygoid teeth as seen in mouth B, and a Diapsid condition of two temporal fenestra as seen in skull B.

We have found enough Mosasaur fossils that scientists have been able to construct hypotheses regarding early Mosasaur evolution. This is a very different scenario from the Ichthyopterygians and Sauropterygians who appear suddenly in the stratigraphic record and have no current record of transitional forms.

1.2 Mosasaur Discovery, Cuvier, And Extinction

While 30,000,000 y seems like a long time, in geologic terms it is very short. Therefore, we need to introduce some smaller units of time in order to clarify our discussion on Mosasaur evolution.

1.2.1 Shortest Unit Of Geological Time

Think back to what you may know about the geological time scale. Try to put the following units of time in order from longest to shortest. Pick the ordering of time units that correctly arranges them from longest to shortest time unit.

A. Period, Era, Age, Eon

B. Eon, Era, Period, Age

C. Age, Period, Eon, Era

D. Era, Age, Eon, Period

As you may know, the Mesozoic is a unit of time known as an era in the Phanerozoic eon. The Mesozoic is divided into the three periods, the Triassic, Jurassic and Cretaceous. Periods spanning millions of years and can be subdivided into even smaller units of time for more precise communication. We call these units' ages. Therefore, the correct answer here is **B**.

1.3 Late-Cretaceous Geologic Ages

The Late-Cretaceous, which spans the entirety of Mosasaurus existence, is divided into six ages, the Cenomanian, which began 100,000,000 y ago, followed by the Turonian, Coniacian, Santonian, Campanian and Masstrichtian, which ended 65,000,000 y ago with the End-Cretaceous extinction event. You should notice that these ages do not represent equal amounts of time.

As we did with the Ichthyopterygians and Sauropterygians, we will begin our exploration of the major Mosasaur groups with the most basal and earliest members of the Pythonomorpha. These are the Dolichosaurs, Pontosaurs, and Adriosaurs. Around 90,000,000 y ago, several lineages of ancient, terrestrial, and guiamorph Lizards took to the water and very quickly became fully aquatic.

Illustration 104: *Adriosaurus Microbrachis* (Fossil)

One of the groups, the Dolichosauridae were small, long-bodied Lizards with long necks, short to medium-sized skulls, reduced limbs, and a very long laterally compressed tail. They lived at the beginning of the Late-Cretaceous in the Cenomanian and Turonian in the near shore reefs around the Northern hemisphere. One particularly interesting specimen was *Adriosaurus Microbrachis*. Although it had well-developed rear limbs, its front limbs had been reduced so much, that only a tiny humorous was left, indicating that its front limbs played no significant role in any aspect of it is life. Another remarkable specimen of Pontosaurs preserved the trachea and scales. The scales were smooth and represented an early adaptation to the aquatic problem of viscous drag.

The earliest basal Mosasauroids are known as the Aigialsauridae. They lived during the Cinemanian and Turonian in Europe and North America. They inhabited shallow marine environments, such as reefs and lagoons, where they would probably have preyed on small Fish and Invertebrates. They were very slender, up to 2 m long, and had extremely long tails that were much longer than the head and body combined. This long, flattened tail would have been their primary source of propulsion. Steering would have been accomplished by their large feet with elongated and slender digits that may have been webbed since these early forms had not yet evolved paddles. In addition, the pakistonic bones of some species would have maintained neutral buoyancy. Their skulls are almost indistinguishable from Mosasaurs, but their bodies more closely resembled terrestrial Lizards.

There are two main sub groups within the derived Mosasaur lineage. On one side is a lineage that contains groups like the Tylosaurinae and the Tethysaurinae, and these Mosasaurs are characterized by simpler limb bones and a lesser degree of ossification in their delicate and more elongate flippers. This means that many wrist and ankle elements remained as simple cartilaginous structures and never became bony. The other major Mosasaur lineage is the Mosasaurinae. They have robust flippers where all the wrist and ankle elements are ossified, blocky, and the limb bones are more complex. Each of this clades is composed of multiple subfamilies or smaller groups of related genre, each with their defining sets of characters. We are now going to explore these groups to learn about their diversity, trace their inner relationships, and discover what makes each one unique.

The basal Mosasauroids in this lineage include *Carsosaurus* and *Komensaurus* who lived during the Cinemania. This Mosasauroids were likely semi-aquatic and retained primitive limbs and pelvic girdle morphologies, that is, they did not have flippers. The only *Carsosaurus* that has been found is particularly interesting as it is a pregnant female containing at least four embryos. Which you can see outlined in this photo. It is the only evidence of viviparity or live birth in basal Mosasauroids, and it shows that viviparity developed early in Mosasaur evolution.

The next most arrive group known from Turonian age deposits also likely retains some primitive terrestrial characters in the limbs and pelvic girdle. One of these groups, the Tephesaurinae is known to have the more typically terrestrial structures of both its limbs and pelvis. For example, the pelvic girdle of Tephesaurus would have articulated to the spinal column, a connection that is lost in more aquatically adopted species. Additionally, most derived Mosasaurs have only a few pterygoid teeth in the roof of their mouth, but Tephesaurus could have as many as 19 pterygoid teeth.

Another closely related group, the Yaguarasaurinae, likely represents the transition from semi-aquatic to fully marine limb morphology. This means it probably had both paddles and unattached hipbones. Unfortunately, no limbs and girdles have yet been found from this group. Therefore, their position as a transitional form is just a guess based on other intermediate features of their skulls. These Mosasaurs were relatively small, usually 3 – 5 m in length and had slender jaws with posteriorly curved teeth.

1.3.1 Order Of Adaptation

The groups we have just discussed show the transition from a terrestrial morphology with well-attached pelvic girdles and weight bearing feet to an aquatic morphology, with loosely attached pelvic girdles and flippers.

In what order did these two adaptations happen? Which scenario do you think is correct?

A. They evolved aquatic flippers then an aquatic pelvis

B. They evolved an aquatic pelvis then aquatic flippers

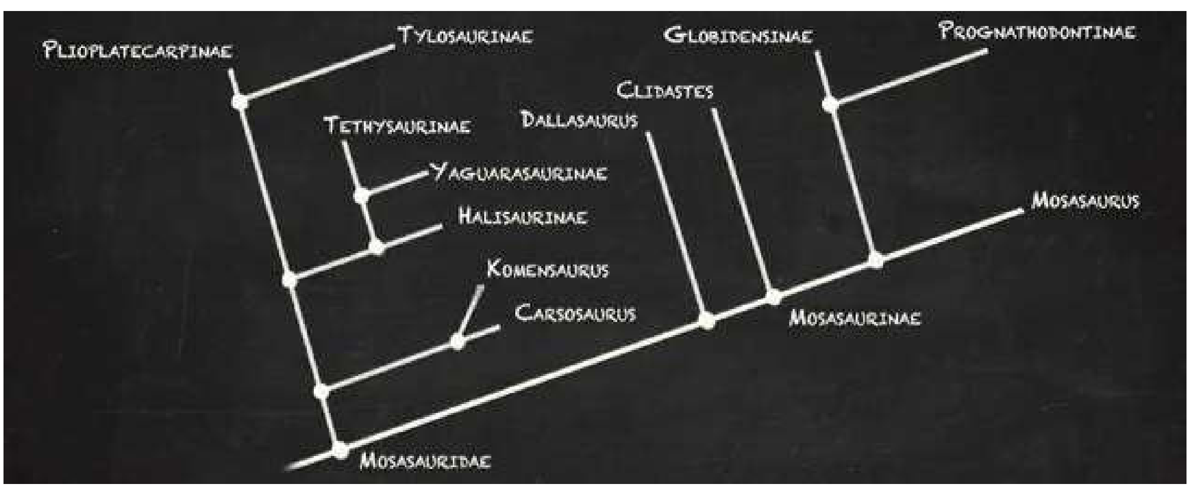
C. They evolved both at the same time.

Evolving an aquatic pelvis while retaining weight-bearing legs would not work, since even though their legs could bear weight, their pelvis would collapse. Therefore, B is incorrect.

Flippers connected to weight bearing pelvis are still functional. Therefore, A could be possible from a logical perspective. C is also unlikely to be correct.

There is more evolutionary pressure on the limbs than the pelvis, because limbs play a bigger role in locomotion. Therefore, limbs tend to adapt faster than the pelvis, which what we see in the Fossil record. Therefore, **A** is the correct answer.

1.4 Mosasauroid Diagnostic Characters



The next group we will discuss is the Halisaurinae. **Halisaurus**, which means **Sea lizard**, is an enigmatic genus of Mosasaur that first appeared in the Santonian. The relationships between this genus and the rest of the derived Mosasaurs have been problematic. Various paleontologists have grouped them on both sides of the Mosasaur tree, or even as separate branches all together. We will follow a recent phylogenetic analysis, which found that Halisaurus was the sister group to the Tethysaurs and Yaguarasaurus, but this is a topic that is still under research.

Even if there is little consensus about where Halisaurines fit in the Mosasaur lineage, their morphology is well documented. Halisaurines range 4 – 6 ms in length, and their skeletons do not exhibit many characteristics indicative that they were highly adapted for swimming. They managed to have a large geographic and stratographic distribution and to surviving from the Santonian to the Maastrichtian and have been found on almost every continent.

Illustration 105: Plioplatecarpinae (Fossil)

The **Plioplatecarpinae** were the longest-lived group of Mosasaurs arising early in the evolution of this lineage and surviving until the End-Cretaceous extinction event. Plioplatecarpines exhibit a very generic Mosasaur body plan with few unique specializations. Their skulls and bodies were usually not very elongated. Their pelvic girdle was reduced and no longer articulated to the spinal column. Their paddle-like limbs only exhibit a modest degree of hyperphalangy with only up to five or six phalanges in their longest digits.

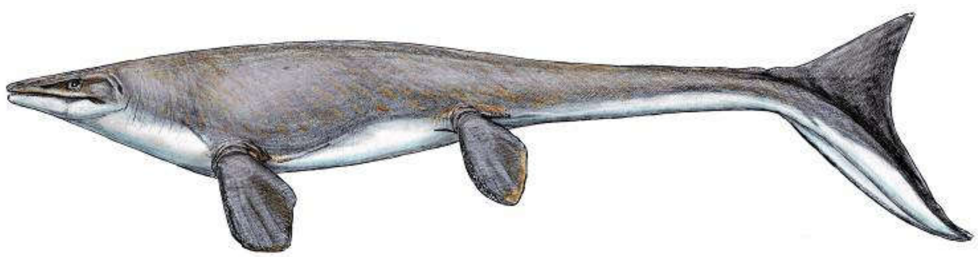


Illustration 106: *Platecarpus* (Live restoration)

One of the earlier Mosasaur in this group is *Platecarpus* that lived during the Santonian. Though medium sized by Mosasaurus standards at 6.5 m, Platecarpus were exceptionally fast and flexible. Their teeth were small, suggesting that they specialized in chasing down Fish and Cephalopods, supported by finds of these types of prey associated with *Platecarpus* fossils.

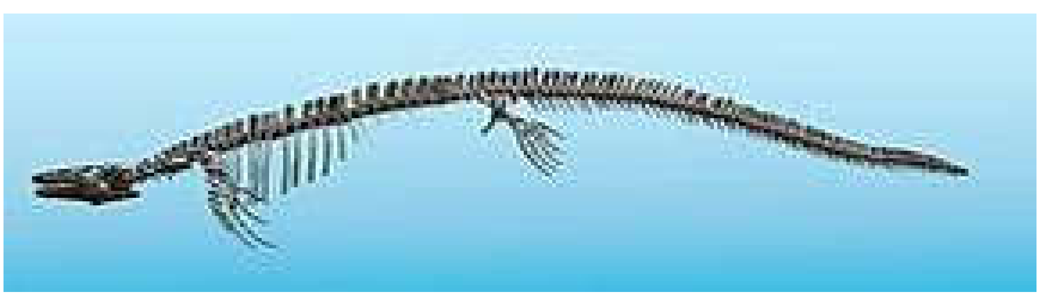


Illustration 107: *Plioplatecarpus* (Fossil)

Members of the genus Platecarpus eventually gave rise to the more specialized form, *Plioplatecarpus*. *Plioplatecarpus* was probably an inhabitant of shallow inshore waters and had the largest brain of any Mosasaur. It is needle-sharp backwards curved teeth suggest that it drew in prey by what is known as **ratchet feeding**. This type of feeding is where the jaw walks down the prey first. The top jaw, and then the bottom jaw moved, until it is been completely swallowed.

Illustration 108: ***Tylosaurus proriger*** **(Live restoration)**

The most derived Mosasaurs on this side of the tree are the **Tylosaurinae**. The first recognized Tylosaurine was *Tylosaurus prorige*. It was up to 15 m long, had heavy jaws, robust, sharp, cone-like teeth; and paddle-like fore and hind flippers. It preyed on Fish, Shellfish, diving Birds, probably smaller Mosasaurs and Plesiosaurs. Tylosaurus translates to Knob lizard, and proriger means prow bearing, names that both refer to the unique elongated rostrum that projected beyond the teeth in the upper jaw. It is been hypothesized that this knob was similar in function to the ram that ancient Greeks and Romans mounted on the prows of their warships to ram enemy vessels. Tylosaurines may have used their snout rams to stun prey, to defend against predators, or to battle rivals of their own species. Weighing at an estimated 8 t this would have been a devastating blow for any creature on the receiving end.

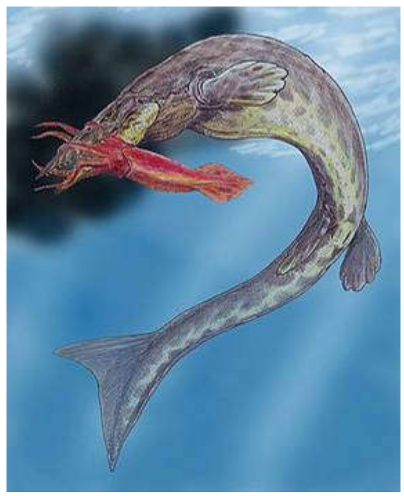
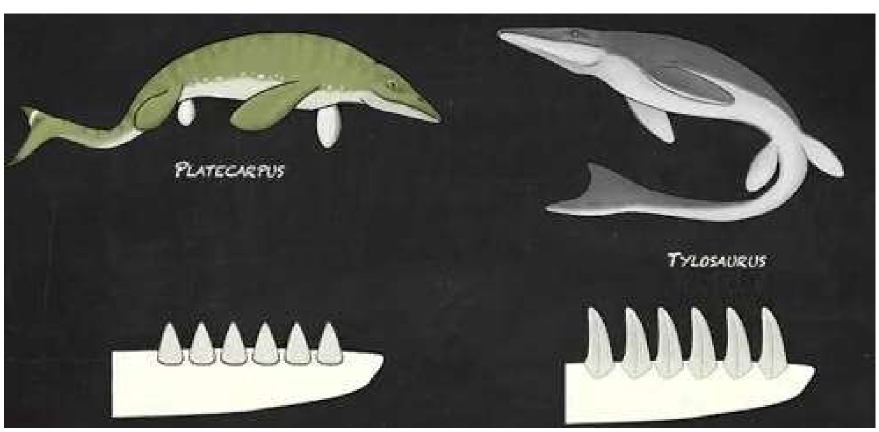


Illustration 109: ***Hainosaurus*** **(Live restoration)**

One of the largest of the Tylosaurinae Mosasaurs was *Hainosaurus*. It could reach a length of >15 m with a skull up to 2 m long. It had 40 vertebrae, not including the tail, compared to the 35 of Tylosaurus. One particular specimen from Belgium demonstrates the degree that which these animals could open their jaws: the carapace of a large Turtle was found in its guts.

Before we move on to the other major Mosasaur lineage, take a minute to review the groups you have just learned about, how they relate to each other, and their progression of adaptations from terrestrial to aquatic.

1.4.1 Swimming And Hunting



We have introduced you to multiple genera from one side of the Mosasaur lineage. Even though they were closely related, a wide variety of forms, functions, and behaviors evolved within this sub-family. For example, compare *Platecarpus* and *Tylosaurus*. *Tylosaurus* was larger, with a large tail and a greater degree of hyperphalangy than *Platecarpus*. Their teeth were also different. *Platecarpus* had small, narrow, smooth teeth, while *Tylosaurus* had large, sturdy teeth with cutting edges.

What do these differences in morphology say about the differences in the way these two Mosasaurs swam and hunted?

A. Both Platecarpus and Tylosaurus ambushed small prey

B. Platecarpus ambushed small prey, and Tylosaurus pursued large prey

C. Tylosaurus ambushed small prey, and Platecarpus pursued large prey

D. Both Tylosaurus and Platecarpus pursued large prey

Tylosaurus exhibited greater hyperphalangy then *Platecarpus*, with nine or ten phalanges in their longest digits, resulting in longer, stiffer flippers that were better adapted for changing direction at speed. Their tails were longer and more powerful, which allowed them to accelerate quickly. The mouth of *Tylosaurus* was filled with large, thick teeth that had cutting edges. These teeth are from the cutting guild we talked about in lesson 2 and are perfect for tearing chunks off from large prey. *Platecarpus* had smaller, more pointed teeth, similar to those in the smash guild. These teeth were too delicate for tearing off large prey, but they were well suited for catching smaller slippery prey like Fish and Squid. Additionally, *Platecarpus* had smaller flippers containing fewer phalanges and a less powerful tail. *Platecarpus* was well-adapted for swimming long distances in search of schools of Fish or Squid that they could ambush. The more powerfully built *Tylosaurus* had the ideal adaptations for chasing down large prey, like Turtles and other marine Reptiles that they could tear apart and consume. Therefore, the correct answer is **B**.

Illustration 110: *Dallasaurus* (Live restoration)

The other main branch of the Mosasauroid tree, the sub-family Mosasaurinae, also is thought to have a primitively limbed Agialosaur at the base. *Dallasaurus* from the Turonian of Texas had feet typical of the terrestrial Lizard as well as a primitive pelvis indicating that both major Mosasaur lineages made the transition from land to sea independently of each other.

Illustration 111: *Clidastes Propython* (Fossil)

Clidastes, the most basal flipper bearing Mosasaurine is also the smallest at a maximum length of 3.5 m. Clidastes appears in the Fossil record at the end of the Coniacian, or beginning of the Santonian, and has a thin elongated body, and the shortest relative tail length of the all the Mosasaurs. It has a short skull with smooth sharp-tip teeth, and a low triangular fin on the upper surface of its tail. It exhibits little hyperphalangy having only as many as five phalanges. This basal Mosasaurine would have very much resembled some of the earliest Ichthyopterygians and Sauropterygians. This is yet another example of convergence, as all these groups seem to get their start in the same way. They first lived in the shallow seas, had long bodies and tails, and four feet that slowly developed into flippers.

Illustration 112: ***Prognathodon overtoni*** **(Skull Fossil)**

Prognathodon was a genus of medium-sized Mosasaur, averaging around 5 m, though some individuals might have been twice that size. This genus was named for having an unusual **premaxilla**, which is a bone that is found in the front portion of the upper jaw. *Prognathodon* means **projecting jaw teeth**, which refers to the way the premaxillary teeth stick out from the front of the mouth. The rest of the mouth was filled with large, ridged jaw teeth and a nasty set of backwards-projecting pterygoid teeth.

Prognathadons are the bulldogs of the Mosasaur lineage, with relatively short blunt skulls. However, the proportions of these skulls to the rest of their bodies, is unusual. While their skulls are massive, and heavily constructed, the rest of their skeletons are much more delicate. It often looks like the skulls should not belong to the bodies.

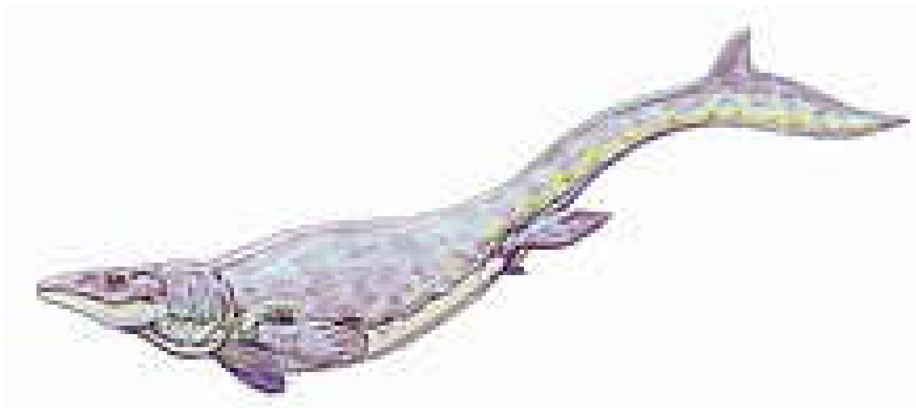


Illustration 113: ***Globidens alabamaensis*** **(Life restoration)**

Globidens, meaning round or globular teeth, is another Mosasaur with a very robust skull. *Globidens* are known for having rounded teeth instead of the Mosasaur typical conical spikes. These Mosasaurs were durophagous, and probably ate only hard-shelled invertebrates. They must have had a lot of them since these animals could reach >6 m in length. A modern analog for this lifestyle is the Horn shark, which has plates in the back of its jaws that are used specifically to crush the hard shells of Oysters and Clams.

Illustration 114: ***Carinodens belgicus*** **(Very rare partial mandible)**

Closely related to *Globidens* and having similarly rounded teeth was *Carinodens*. These Mosasaurs generally considered the sister group to *Globidens* were only 3 – 4 m long and probably searched the sea floor for small Mollusks and Sea urchins to eat. Most phylogenetic analyses find *Globidens* and *Carinodens* to be closely related to Prognathadons due to the similarity of their quadrate morphology.

Globidens and *Carinodens* are the first marine Reptiles since the Sauropterygian Placodonts and the Ichthyosaur *Grippia* of the Triassic that were specialized for feeding on shelled animals. They are also the only Mosasaurs that do not have pterygoid teeth in the roof of their mouths, which were likely lost since their shelled prey was not slippery and did not struggle as it was eaten. Other Mosasaurs, such as *Prognathodon*, have also been found with the occasional hard-shelled animal remains in their stomachs, but in these forms, it was probably opportunistic and part of a wider feeding strategy.

The namesake of the Mosasaurinae, the group that includes *Clidastes*, *Prognathodon* and *Globidens* is the genus Mosasaurus, which includes the original Maastricht species we discussed at the beginning of this lesson. This genus includes large Mosasaurs, usually ranging in length 7 – 15 m long. This group has been found in Campanian and Maastrichtian strata all over the World. Mosasaurus had strong teeth with a pair of cutting edges running along their lengths like some carnivorous Dinosaurs, such as *Tyrannosaurus rex*. The limb bones and phalanges of Mosasaurus were large and blocky, indicating that the paddle would have been quite rigid, and they had a moderate degree of hyperphalangy.

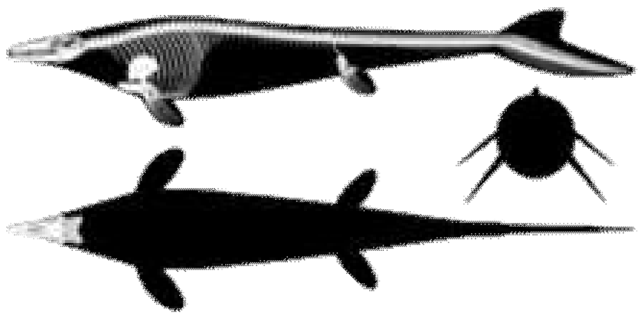


Illustration 115: *Mosasaurus hoffmanni* (Fossil reconstrution)

Mosasaurus hoffmanni was one of the latest and largest of the Mosasaurs reaching lengths of >17 m. Its skull was pointed with the nostrils retracted from the end of the snout to facilitate breathing. The multi-faceted teeth were more complex than those of earlier Mosasaurs, and extremely effective at cutting through or dismembering prey. Its enormous size, along with its powerful jaws and teeth meant that almost any creature was a potential meal.

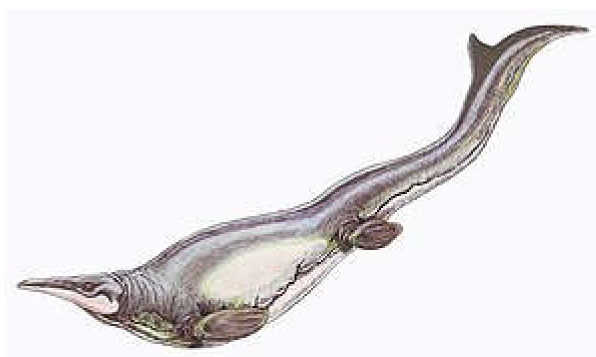
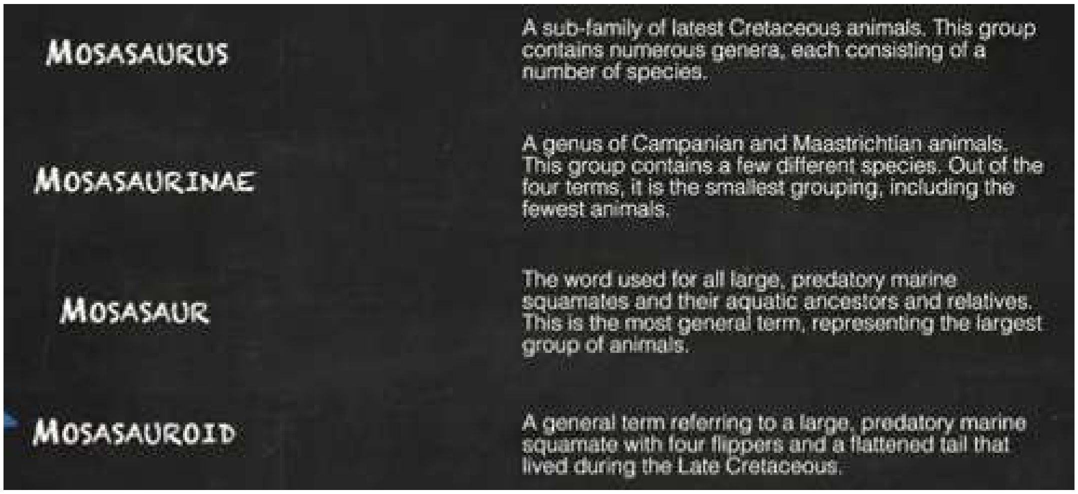


Illustration 116: *Plotosaurus bennisoni* (Life restoration)

One of the most derived Mosasaurs, known from the Maastrichtian of California is *Plotosaurus*. The exact position of Plotosaurus in the Mosasaur phylogeny has been a source of conflict, but it appears to be closely related to Mosasaurus, and this Mosasaur is quite unusual. The skull is elongated, and the teeth are narrow and densely packed in the jaw. The pterygoid teeth in the roof of the mouth do not point down and back into the throat, but out to the sides of the mouth instead. The limbs are true flippers with a relatively high aspect ratio for a Mosasaur and up to 16 phalanges in the longest digit. The vertebrae in the tail are also unusually specialized for propulsion and likely supported a significant fin. Overall, Plotosaurus might have looked more like an Ichthyosaur than a typical Mosasaur. It may have even behaved like one, swimming the Oceans in search of schools of Fish.

Who knows?

The terms Mosasaurus, Mosasaurinae, Mosasaur, and Mosasauroid all share the same root, Mosasaur, which means Lizard from the Mosa River. Even though they sound the same, these words each refer to more and less general groups of the Lizards we have been discussing. Think back to what you have already learned in this lesson and see if you can match each term to its definition. Let us take a minute to think about the four terms, Mosasaurus, Mosasaurinae, Mosasaur, and Mosasauroid.



The most general of the four terms is Mosasauroid. This word refers to all the marine Reptiles we discussed so far in this lesson. It includes all of the well-adapted aquatic predators in addition to all of their ancestors and relatives within the Mosasauroids or the Mosasaurs.

Mosasaur is a general term used for all the large predators with advanced aquatic adaptations. Therefore, the small, semi-aquatic Aigialosaurs would not be considered Mosasaurs, even though they are Mosasauroids. Remember that there are two major lineages of Mosasaurs, one of which is the sub-family Mosasaurinae.

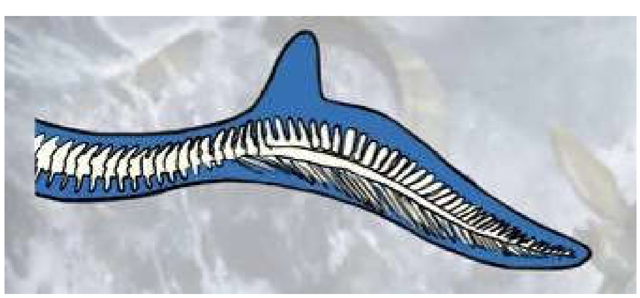
This group includes genera such as *Prognathodon*, *Clidastes*, and *Mosasaurus*. *Mosasaurus* is the least inclusive of the terms since it contains only five species. Any species of Mosasaurus is found in the sub-family Mosasaurinae, which is a type of Mosasaur, which all belong in the Mosasauroid lineage.

Since the discovery of the first Mosasaur fossils in the 1700s it was always assumed that the various groups of Mosasauroids we have just introduced you to, all descended from one ancestral Lizard that returned to the Ocean. However, recent research calls this long held assumption into question. As we have discussed in this lesson, at the base of each of the branches of derived Mosasaur clades there are one or two species, whose limbs or pelvic girdles retained some terrestrial capabilities. Paleontologists are now working on the hypothesis that the two major Mosasaurs lineages had different semi-aquatic ancestors, and that the two groups evolved independently, but parallel to each other. If this were the case, it would be an example of how convergent evolution in closely related groups can lead to similar species responding to similar challenges in similar ways. Whether they are a monophyletic clade or sister groups, they face the same environmental challenges and develop similar solutions. Let us now go on to explore how these marine Reptiles solved the aquatic problem.

1.5 Mosasauroid Phylogeny

The extraordinary sequence of well-preserved material spanning the 30 – 35 million-year history of Mosasauroids shows a steady pattern of adaptation from a terrestrial Lizard anatomy to a highly specialized suite of marine adaptations that are very similar to the Ichthyopterygians and Sauropterygians. This is yet another example of convergent evolution between the unrelated groups of marine Reptiles.

Like early Ichthyopterygians from lesson 2, the basal Pythonomorphs we examined previously in this lesson, such as *Dolichosaurus*, were almost certainly anguilliform swimmers. Their long, slender bodies, flexible vertebral columns, and laterally flattened tails are the same features seen in almost all other anguilliform swimmers we have examined in this course, such as Thalattosaurs and Pachypleurosaurs. Originally, it was thought that the derived Mosasaurs were also anguilliform swimmers, with their entire bodies moving in sinusoidal motions like a Snake or Eel. The absence of Fossil evidence suggesting other forms of locomotion, such as a caudal fin, was used to support this conclusion.



Recent analysis of the structure of their vertebrae has revealed that Mosasaurs became carangiform swimmers. Meaning that the forward part of their body was stiff, while the rear portion undulated, similar to the way Alligators and Cod swim, and this change in swimming style from anguilliform to carangiform is reflected in the changing tail morphology. The vertebral column lost its flexibility, making the body stiffer. The caudal, or tail region, became more specialized, and over time, a downward kink developed in the caudal vertebrae. A cartilaginous blade developed on the top surface of the bend, and like the Ichthyosaurs before them, the Mosasaurs evolved a heterocercal tail. This means that the upper and lower lobes of the tail were different lengths. In Mosasaurs, the lower lobe got much longer and was supported by vertebrae, while a blade of cartilage supported the shorter upper lobe.

Although shorter than in the more basal forms, the muscular tail of derived Mosasaurs was still 42 – 50 % of their body length. The tail was laterally flattened with a lobed heterocercal fin. This resulted in a higher surface area to push against the water. The base of the Mosasaur tail would have been relatively inflexible and would have provided a stable anchor for strong musculature.

1.5.1 How Mosasaurs Swam

You have learned a lot about the morphology of marine Reptiles, and how it relates to their ecology in the past few lessons. Based on the information you have just been given about Mosasaur tail morphology, pick the description below that best fits how you think they would have swam.

A. Long distance open water cruisers

B. Short distance open water cruisers

C. Short distance high-speed swimmers

D. Long distance high-speed swimmer

Mosasaur tail morphology, though extremely powerful, is not particularly energy efficient over a long period of time. It is unlikely that Mosasaurs were as fast over long distances as the Pliosauromorphs or thunniform Ichthyosaurs, but where they did excel was in bursts of high-speed swimming. They could use their enormously powerful tail to accelerate very quickly and maintain a high speed over a short distance. This made them extremely efficient ambush predators, using powerful acceleration and the element of surprise to overtake and capture prey. Therefore, **C** is the correct answer.

The ambush tactics employed by Mosasaurs required them to be able to change direction very quickly. Their large and powerful flippers would have contributed to steering. Differences do exist in the morphology of the limbs between different Mosasauroids, which could be important indicators of their ecology.

In most early Mosasauroids, such as the Agialosaurs, the widely spread, thin bone digits would probably have been loosely joined by webbing to form a flexible flipper. In later genera, such a *Plotosaurus*, the thicker digits were arranged tightly together to form a stiff, wing-like flipper, somewhat resembling Ichthyosaurs and Plesiosaur flippers. Still other genera, such as *Tylosaurus*, the flippers were less ossified and more cartilaginous and highly flexible. Though we are still not precisely sure what these differences meant for Mosasaur locomotion, paleontologists are confident that the flippers were not used for propulsion. Most likely, the flippers were held close to the body, reducing drag, while the tail powered the animals through the water, and were only extended to help steer when the Mosasaur needed to change direction.

This change in morphology in the tail and appendages reflects a progressive shift from lagoonal dwellers to near-shore paddlers to transoceanic animals capable of high-speed attack. These patterns of evolution are similar to those observed in marine Crocodiles, Ichthyopterygians, and the Sauropterygians from former lessons, and to extant groups like Whales.

All of these secondarily aquatic Tetrapods face the same evolutionary pressures when they return to the Ocean. As a result, the evolutionary stages that they progress through, along with the most efficient derived forms, show a great deal of convergence. Mosasaurs, like Sauropterygians and Ichthyopterygians, developed a streamline body, lost their terrestrial fingers, and developed a fused flipper. Like the Sauropterygians, Mosasaurs never developed a dorsal fin, but like the Ichthyopterygians, and the Whales, they maintained axial locomotion.

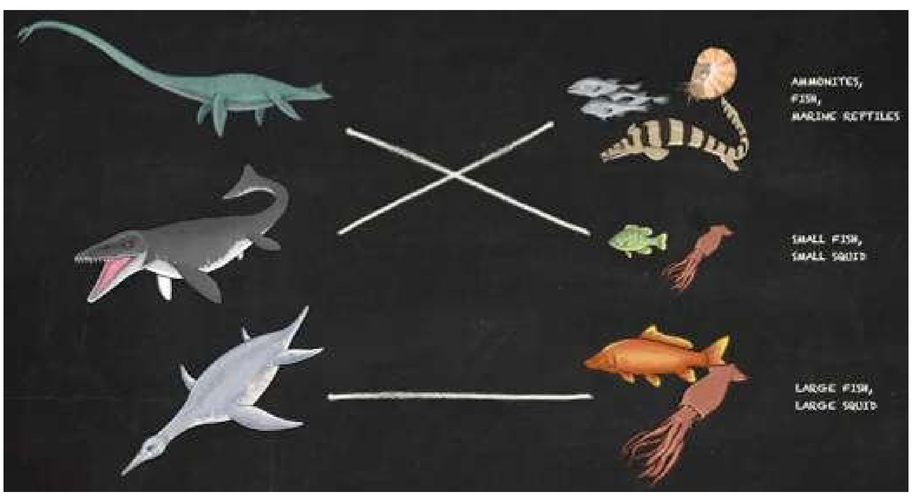
However, like the other major marine reptile groups we have discussed, Mosasaurs developed some solutions to the aquatic problem that were entirely their own. One solution was to retain scales, which Ichthyopterygians and Sauropterygians appear to have lost. Mosasaurs scales are well known for numerous fossils, some of which are exceptionally well preserved. They had small overlapping scales, which would have looked very similar to a Snake. The scales are diamond shaped, and some had a raised ridge down the center. It may seem that these scales would not be as efficient in aquatic adaptation as smooth skin.

However, the small ridges on the scales may actually have reduced the amount of viscous drag by maintaining a thin layer of water around the animal. The ridges and the scales would trap water against the body, and that way, as the Mosasaur moved, friction would be generated between water and water, instead of between water and the animal's body. This resulted in much less drag, and it is similar to the way a Shark's skin works.

Sometimes these scales can even show which sections of the body were darkly colored, which ones were lightly colored. This indicates that some species of Mosasaurs may have had bands of dark and light shading over their bodies. Similar patterns in modern animals, such as Tiger sharks, help to break up the light hitting the animal, making them harder to see, and therefore, better ambush predators.

1.5.2 Specialized Prey Types

Mosasaurs were sharing the seas with Sauropterygians, such as the long-necked Elasmosaurs and the large-mouthed Polycotylids. In order to co-exist, each of these groups specialized on different types of prey. See if you can match the marine reptile to its prey. As we have just discussed, derived Mosasaurs were powerful sprinters and ambush predators. Like other marine Reptiles, these aquatic predators needed to adapt feeding strategies that allow them to acquire and swallow prey in the aquatic environment.



Recall that for long necked Plesiosaurs, food was fairly small and was swallowed completely. Therefore, small Fish is the correct answer. The large mouthed Polycotylids ate correspondingly larger prey, but their narrow teeth and jaws restricted their diet to soft-bodied prey. Therefore, the correct answer is big Fish and Squid. Mosasaurs, with their massive teeth and jaws that were 10 – 14 % of their body length, were able to snap up small prey, crunch through hard prey, or dismember prey too big to swallow. They were opportunistic feeders who could have eaten anything they came across, including other marine Reptiles. Therefore, the correct answer is Ammonites, Fish, and marine Reptiles.

In order to be able to eat such a wide variety of large prey, Mosasaurs needed special adaptations in their skull. One such adaptation unique to Mosasaurs was their **highly-kinetic** or flexible skulls and jaws. Together, flexible elements such as the inter- and intramandibular joints would have allowed Mosasaurs to open their jaws wide enough to swallow large prey.

The intermandibular joint allows the two sides of the jaw to separate slightly, and the intramandibular joint and quadrates allow the mouth to expand. The extra space created by all these joints would allow the Mosasaur to fit large prey into its mouth. Once in the mouth, the curved pterygoid teeth in the throat would prevent any prey from struggling away.

Even with their impressive gape, sometimes the prey was indeed too large to swallow. Some of the larger Mosasaurs, like *Tylosaurus* and *Prognathodon*, ate other marine Reptiles such as Turtles, Plesiosaurs, and smaller Mosasaurs. It is thought that these large Mosasaurs could have dismembered their prey by shaking it like a Shark. Having highly flexible skulls is not advantageous when feeding in this way, and therefore, in many larger Mosasaurs the skull became less and less kinetic.

The flexibility of the skull is not the only adaptation Mosasaurs developed that enabled them to consume large tough prey. Their teeth, the tools used to actively tear, crush, and dismember their prey, also developed specialized growth patterns. You are probably most familiar with the typical mammalian tooth growth pattern of developing one set of teeth as an infant, and a second set of replacement teeth through maturity. Mosasaurs grew teeth continuously throughout their lives with replacement teeth growing beside the functional teeth. Each replacement tooth would develop behind the functional tooth, slowly dissolving the base of the old tooth until it fell out, and the new tooth move into the socket to become the new functional tooth. This is a typical pattern of tooth replacement for all Lizards and Snakes. Tooth replacement was especially important for Mosasaurs that ate harder prey items, because hard-shell prey wore down their teeth faster, making the teeth less effective. Tooth wear is found in Mollusk crushers like Globidens and Carinodens, and can also be seen on the tips of the large pointed teeth of Mosasaurus.

1.5.3 Tooth Wear

What were the Mosasaurs biting that would have worn down the tips of their teeth? Select which of the following prey you think would have caused the most wear to Mosasaur teeth.

- **A.** Fish
- **B.** Squid
- **C.** Marine Reptiles
- **D.** Ammonites

Though Mosasaurs commonly ate Fish and Squid, they were soft bodied and would barely have worn down the teeth. Therefore, A and B are not correct.

Marine Reptiles, with their thick bones, would have caused some damage to the teeth, but was probably not the main cause of tooth wear. Therefore, C is not correct.

One of Mosasaurs most common prey items, and one of the toughest to eat, was Ammonites, common invertebrates in the Mesozoic Oceans. Several fossils of the round disc-like Ammonites have been found with an odd pattern of holes in the shells. These holes can be connected to form a large V shape. The size of the V and the spacing between the holes corresponds well with the arrangement of teeth in a large Mosasaur jaw.

Some of these bitten Ammonites even have multiple sets of teeth marks as if the Mosasaur bit in and either could not chew it or could not swallow it, and therefore, the Mosasaur released the ammonite to try again. Paleontologists debate whether Mosasaurs swallowed Ammonites whole and let the shells dissolve in their stomachs, or whether they crushed the Ammonite shells with their teeth to get to the soft animal inside. Either way, the hard shells of the Ammonites would have caused considerable wear to the teeth. Therefore, **D** is the correct answer.

The Ammonites, and other large prey items on the Mosasaurs' menu, were not always easily found in surface water. Therefore, Mosasaurs would have to dive to hunt. Think back to the types of Fossil evidence that had been used to infer which Ichthyosaurs were deep divers. This includes their eye size and regions of collapsed bony tissue attributed to avascular necrosis. While no Mosasaur had eyes as large as some Ichthyosaurs, evidence of avascular necrosis has been found in some species.

For example, the genera Clidastes, Platecarpus, and Tylosaurus are known to have co-habited the Western Interior Sea, which covered the middle of North America. This seaway was relatively shallow, likely less than 200 m. Nevertheless, 200 m is deep enough to result in the pressure changes that release dissolved gasses from the bloodstream if ascent is too rapid. Avascular necrosis is never seen in Clidastes, but has been found in Platecarpus and Tylosaurus. Clidastes, with its less specialized morphology is therefore thought to have inhabited shallower waters, whereas Platecarpus and Tylosaurus pursued prey in the dark Ocean depths.

1.5.4 Mosasaurs Seeing

Even though their eyes are not as adapted as Ichthyosaurs, Mosasaur senses were still highly adapted to solve the aquatic problem. Though not as proportionately large as Ichthyosaurs, they still had fairly large eyes that were probably useful for seeing in dimly lit waters. Mosasaurs also had sclerotic rings, which are used to support the eyeball and to change its shape in order to focus the eye. The large eyes faced laterally from the head, giving the Mosasaur a wide range of vision, but would have prevented binocular vision and limited depth perception. Some paleontologists have hypothesized that, like Snakes and Lizards, Mosasaurs may have had a transparent eyelid covering their eye to protect them and prevent water loss from the eye by osmosis.

The ears in Mosasaurs are also well-adapted to their environment. Recall that in water eardrums are not particularly good at detecting vibrations, therefore, many aquatic Amniotes hear by picking up vibrations in the water through their skull bones. This is a type of hearing called **bone conduction**. Mosasaur ears have gone one-step further and have evolved a hard, cone-shaped, bony formation that sat where the eardrum was in their terrestrial relatives. This cone-shaped plate would have picked up sound in the water, focused it, and directed it towards the inner ear far more effectively than the skull bones. This would have given Mosasaurs a fairly acute sense of hearing under water. A similar modification is seen in Whales.

1.5.5 Mosasaurs Hearing

What purpose would an acute sense of hearing serve in Mosasaurs? Check all that might apply.

A. Detecting prey

B. Locating threats

C. Finding mates

D. Echolocation

Since smell transmits so poorly in water, Mosasaurs almost certainly used their sense of hearing and sight to detect their prey and potential threats, therefore, **A** and **B** are correct. Additionally, while no evidence has been found, it has been hypothesized that Mosasaurs, which were likely solitary, would have used acute sense of hearing to communicate between other members of their species. This would have been especially important in helping them locate a mate across long distances in the open Ocean. Therefore, **C** is correct.

We have no evidence of any reptile evolving ever specializations for echolocation. Therefore, D is incorrect. This type of logical deduction often is part of the process within paleontology.

Mosasaurs, like the Ichthyopterygians and Sauropterygians we have already talked about, were viviparous and bore live young. A Fossil of the basal Mosasauroid, *Carsosaurus*, which was found with at least four advanced embryos in the abdomen, indicates that this adaptation to the aquatic lifestyle developed early in their evolution. The orientation of the embryos suggests that they were born tail first, like the Ichthyosaurs and modern Whales, to reduce the possibility of the newborns drowning before they were separated from the mother. Viviparity in these early, medium-sized, amphibious Mosasauroids freed them from returning to the land to deposit eggs, permitting the evolution of gigantic, fully-marine Mosasaurs.

One of the best places to study juvenile Mosasaurs is the **Smoky Hill Chalk** and the **Niobrara Chalk** in Kansas. A large number of small Mosasaurs had been found in this location, which would have been in the middle of the Ocean in the time of the Mosasaurs. Like the Sauropterygians, the fact that Mosasaurs were apparently giving birth mid-Ocean means that the mothers were probably heavily invested in their young. The mothers gave birth to a small number of well-developed offspring, and they probably would have protected and helped feed them until they matured. Even with parental care, the survival rate of young Mosasaurs was probably low in an environment shared with large Sharks, giant Fish, and other Mosasaurs.

1.5.5.1 Paleopathology

An additional source of data used to infer aspects of the lives of extinct animals is **paleopathology**, or the study of diseases or injuries as preserved in fossils. We have already discussed one form of paleopathology, the bony tissue deterioration called avascular necrosis, which results from ascending too quickly during a deep dive. Paleopathologies can record diseases such as arthritis and bone cancer. Physical trauma such as broken bones or bite marks and even evidence of healing.

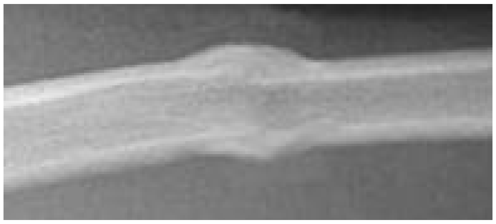
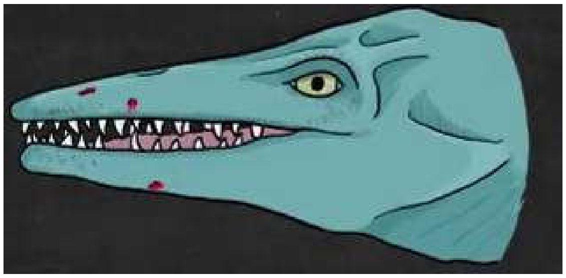


Illustration 117: Bony callus (X-ray photo)

A bony **callus** is an extra growth of ossified tissue, which grows around the site of an injury. Such a callus around a break or bite mark indicates that the animal lived long enough after the incident for its injury to heal. On the other hand, if there are no signs of new bone growth around the injury then it is possible that the incident contributed to the individual's death. Broken bones are usually not fatal to humans, but are fatal for many animals since they impair their ability to hunt, and evade predators. Mosasaur fossils have been found that preserve a wide range of paleopathologies, including diseases like avascular necrosis, infections of bony tissues, and various injuries. Interestingly, Mosasaur paleopathologies tend to be concentrated around the skull and jaws. This could be the result of collection bias resulting from more skulls then bodies in paleontological collections. However, some Mosasaur jaws have been found with bone that had been healed around very clear bite marks. This suggests that injuries to the head were common for Mosasaurs and may indicate some interesting behaviors that paleontologists are just starting to investigate.

1.5.6 Bite Marks On Mosasaurs

Take a close look at this Mosasaur skull and jaw as it clearly shows bite marks.



What type of behavior do you think these bite marks on the head and jaw suggest? Remember that paleontologists often have to take the most logical path based on the evidence provided. Select all that apply.

A. Mosasaurs preying on each other

B. Mosasaurs fighting each other for resources

C. Mosasaurs fighting with Pliosaurs

D. Mosasaurs being preyed on by Sharks

It is unlikely that paleontologists will ever know for certain how or why these Mosasaurs got bitten. However, it does appear that they resulted from being bitten by another Mosasaur. While Sharks certainly bit Mosasaurs, Shark teeth do not match the shapes of the preserved bite marks; therefore, D is not correct.

Pliosaur teeth are a better match shape wise, but Late-Cretaceous Pliosaurs were much smaller than the injured Mosasaurs, therefore, C is not correct.

The bite marks do match Mosasaur teeth and likely came from an individual about the same size as the one that was bitten. This is probably not an example of attempted Mosasaur cannibalism, answer A since even Mosasaurs would avoid prey as big as they were. It is just too dangerous. The most likely answer is, therefore, **B**. Mosasaurs fighting each other for food, territory, or mates.

Illustration 118: *Mosasaurus* jaw with embedded *Mosasaurus* teeth

As you just discovered the wounds on Mosasaur skulls are considered to be a record of **intraspecific** interactions or occasions when individuals of the same species came into contact. Intraspecific aggression is supported by scratches and puncture marks and also by a few rare fossils that preserve the aggressors broken off tooth still embedded in the bone.

One of the genera that exhibit several cases of bites around the skull and jaws is *Mosasaurus*. It is most likely that only another *Mosasaurus* would have been able to attack the large individuals that had been found injured. The bites could have been inflicted during competition for food, territory, mates, or even during the mating process.

Evidence of **interspecific** interactions occurs when individuals of different species came into contact. For the most part, these are easier to interpret, because they come in the form of stomach contents. Large Mosasaurs had been found with smaller Mosasaurs in their stomach cavities. Unlike the specimens that provided evidence of live birth, in Plesiosaurs and Ichthyosaurs, stomach contents show fragmentation and erosion from stomach acid, meaning that they were processed and partially digested. The strongest evidence of Mosasaurs preying on each other is when smaller Mosasaurs in the stomach are complete enough for identification and are different species than the larger Mosasaur that ate them.

Mosasaurs evolved relatively quickly from small shore dwelling Lizards into the dominant marine predators of Earth's Oceans. Live birth freed the Mosasaurs from the constraints of terrestrial living, allowing them to evolve into the ultimate predator of the Cretaceous seas.

Their adaptations to life in the Ocean included major modifications to the axial skeleton and limbs, including a long body and tail with a heterocercal fin and strong flippers in a variety of shapes. Mosasaurs also had small scales covering their body that decreased drag and may have had shading that made them harder to see. The highly kinetic skulls and jaws of some species enable them to swallow larger prey than any previous marine reptile, and wickedly pointed pterygoid teeth prevented the escape of any prey unlucky enough to be bitten.

Even animals that were too big to be swallowed were not safe. Derived species of Mosasaurs with less kinetic skulls became adapted to tearing and dismembering extremely large prey. With acute senses of hearing and sight, not much would have escaped these supremely well-adapted predators, the undisputed rulers of the late Cretaceous seas. Fossil evidence in the form of broken bones and bite marks shows that only another Mosasaur was big or powerful enough to challenge these Reptiles.

The next section will give us an overview of the extent of Mosasaur dominance. We will explore the patterns of their diversification and distribution as they became better and better adapted to solve the aquatic problem. We will also introduce you to some famous localities where Mosasaur fossils have been found.

2 Mosasaur Paleobiology

Mosasaur evolution appears to have occurred in three distinctive waves, each better adapted to solve the aquatic problem than the one before. The first wave occurred in the Coniacian in the Western Interior Seaway, with the evolution of Mosasaurs that had developed aquatic adaptations, but still possessed terrestrial features. Mosasaurus continued to evolve growing larger, diversifying rapidly, and adapting solved the aquatic problem even better. About 83,500,000 y ago a second wave of new forms appeared near the beginning of the Campania. Following a possible decrease in diversity near the middle of the Campanian Mosasaurs rebounded, and a third wave of highly aquatically derived Mosasaurs, more diverse and numerous than any before was just getting under way in the Maastrichtian, shortly before their extinction.

For the last section, let us look at the incredible rate of evolution and dispersal of Mosasaurs and the records of their success that can be found on every continent.

2.1 Mosasaur Transition

2.1.1 Late-Cretaceous

Earth at the start of the Late-Cretaceous was very different than it is today. The climate was several degrees warmer. As a result, there were no polar ice caps. The extra water in the Oceans flooded the continents, forming shallow seas across Europe, North America, Africa, Australia, and India. It was into this environment that the ancestors of the Mosasaurs began their transition to the seas.

Which of the following factors do you think would have made this transition more likely? Choose all that apply.

A. The water temperatures were higher

B. There were fewer predators in the Ocean

C. Eggs were more likely to survive in the water

D. There were lots of shallow reefs and coastlines

We may never know exactly why these squamates first entered the Oceans. However, there are a couple of factors that probably would have made their transition more likely. The Ocean temperatures of today are too cold for most Reptiles. This is why the majority of extant, aquatic, or semi-aquatic, Reptiles are found near the equator. In the Late-Cretaceous, the water would have been several degrees warmer, especially in the shallow continental seas. This would have made it easier for Reptiles to live in this environment. Therefore, **A** is correct.

This time predators were common on land and in the water, leaving the land for an environment they were not as well-adapted for would probably not have made them any safer. Therefore, B is incorrect.

The amniotic egg is filled with small pores for gas exchange. Under water, these pores get blocked, and the developing embryo suffocates. Therefore, C is also incorrect.

The greater amount in reefs in coastlines in the Late-Cretaceous increases the area, and therefore, the probability that a squamate could invade this environment. Therefore, D is also correct.

2.1.2 Mid-Cretaceous

By the Mid-Cretaceous, about 90,000,000 y ago, the continents were arranged roughly where they are now. Except, that Australia was still attached to Antarctica, and India still attached to Madagascar, had not yet begun its northward journey towards Asia. Worldwide sea levels were 90 – 150 m higher than they are today, covering a third of all presently exposed land. Much of North America and Europe were underwater, covered by the shallow Western Interior Sea and Tethys Sea, respectively.

It was in this warm, wet World that the Mosasaurs began their colonization of the World's shallow waters. The Mosasaurs did not enter a realm devoid of predators, since the Ichthyosaurs and Plesiosaurs had colonized the Oceans long before the Mosasaurs did. However, the Ichthyosaurs were in decline by the time the Mosasaurs evolved.

Many researchers believe that the disappearance of the Ichthyosaurs was caused by competition with the larger, more powerful Mosasaurs. However, it is unlikely that the first small-bodied Mosasauroids would ever have seen an Ichthyosaur, since the earliest Mosasauroids lived in shallow reefs, and the last Ichthyosaurs were only found in the open Ocean.

2.1.3 Cenomanian

Basal, semi-aquatic Mosasauroids are primarily known from Tethyan deposits from the Middle-East through Southern Europe, which in the Late-Cretaceous were covered with reefs and islands. *Aigialosaurus* is known from Croatia in a related form, *Carentonosaurus* is common in Cenomanian deposits across France and Spain. Multiple species have been found in Slovenia, including *Cominosaurus* and *Parsosaurus*. These small semi-aquatic Lizards were very diverse and would have spread easily across the World from their European, African origins during this time when shallow seaways covered most of the continents.

2.1.4 Turonian

By the Turonian, Mosasauroids were relatively widespread across Europe and North America. Basal Mosasauroids, like *Dallasaurus*, are known from the Gulf of Mexico. It was during this time that derived Mosasaurs first appear in the Fossil record of the Western Interior Sea of North America. Though fully aquatic, with a number of adaptations to the aquatic problem, they still retain terrestrial features, such as their hips. These fossils are found in Middle-Turonian deposits in Kansas, and are approximately 90,000,000 y old. Later deposits show that by the end of the Turonian, Tethysaurines and Yaguarasaurines lived in shallow seas of today's Italy, Morocco, Texas, and Columbia. Tylosaurus remains have been found in Mexico, Prognathodon in France and Platycarpus in Brazil. Other fragmentary Mosasaur fossils had been found around the World, and even though they cannot be identified precisely, they indicate that Mosasaurs were already, after barely 10,000,000 y, taking over the World's Oceans.

2.1.5 Coniacian

By the Middle-Coniacian, the first major wave of Mosasaurs was well established around the World. *Yaguarasaurus* still inhabited the Oceans around Colombia and Platycarpus has been found in Brazil. Mosasaur fossils are not abundant from the Coniacian of Europe, but specimens of Tylosaurus have been found in France from this time. The Western Interior Sea was inhabited by various species of specialized Mosasaurs. Tylosaurs, Plioplatecarpines and Clidastes all lived in the Western Interior Sea at the same time. In order to coexist, each species likely filled different environmental niches to avoid being in direct competition with each other. This was a pattern that continued throughout the rest of the Cretaceous. Let us investigate what this could have looked like.

Fossils of Clidastes, Tylosaurus, and Globidens are all found in the Western Interior Sea, in the Santonian. Each of these Mosasaurs would have had to focus on different types of prey, in order to avoid competition with each other.

Based on the clues I am about to give you, try to place these three Mosasaurs in their preferred hunting environments.

Globidens and Clidastes have been found in the presence of small Turtles, small Pterosaurs, and toothed Birds. This indicates that these Mosasaurs lived in shallower waters, near the shoreline. The bulbous, crushing teeth of Globidens indicate that its preferred hunting environment was on the bottom of shallow water areas where it could find the hard-shelled Mollusks that it was specialized. Clidastes was not specialized for bottom feeding or for open Ocean hunting. It probably fed primarily on Squid, Fish, and other small vertebrates in shallow water.

The stomach contents of Tylosaurus show that it had a varied diet of near shore and open water prey including Fish, Sharks, smaller Mosasaurs, Plesiosaurs, and diving Birds. This indicates that Tylosaurs hunted in both shallow and deep waters. This is supported by the fact that it has been found in near shore and off shore sediments. However, it was best suited for deep open water hunting further from the shore.

2.1.6 Santonian

The Santonian represents a time when larger Mosasaurs became increasingly common worldwide. The largest number of Santonian Mosasaur fossils has been collected in Kansas, from the formation known as the Niobrara chalk. About 180 m thick, this layer extends from Kansas in the US to Manitoba, Canada, and represents a time about 87 - 82 million years ago, when the Western Interior Sea covered most of Midwestern North America.

A 1993 estimate states that this layer had produced almost 2,000 Mosasaur specimens from Kansas alone. Fossils of Clidastes, Halisaurus, Platecarpus, and Tylosaurus have been found in the Niobrara Chalk and from other deposits of similar age around the Western Interior Sea. Santonian age deposits from Europe tell us that the Tethys was inhabited by Halinosaurus, Plioplatecarpus, and Tylosaurus. However, these giants were not the only Mosasauroids inhabiting these waters.

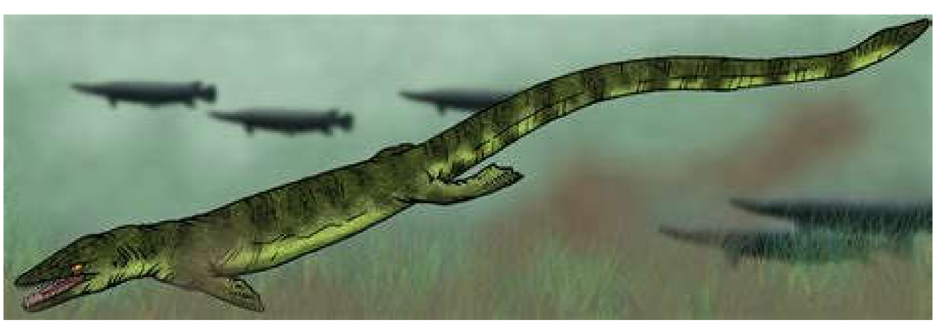


Illustration 119: *Pannoniasaurus* (Life reconstruction)

Smaller Mosasauroids, such as the Hungarian Mosasaur, *Pannoniasaurus* reminds us of the continuing diversity of smaller forms that continue to thrive in shallow water environments. Southern hemisphere Mosasaurs of this time includes Halisaurus from Peru, and Platecarpus from Australia. The Campanian is the longest stage in the Late-Cretaceous, spanning 11,500,000 y. The duration of the Campanian is reflected in the prolific Fossil record from all around the World. The abundant fossils from this time show the diversity that constitutes the second major wave of Mosasaur evolution, represented by large species that had lost all ties to the terrestrial environment.

The Western Interior Sea began to recede to the North during this age, separating the Gulf of Mexico from the rest of the Western Interior, and the separation of these two bodies of water meant that evolution started to take different paths in each of these seas. This resulted in different communities of Mosasaurs in each environment. Both, the Gulf of Mexico and the Western Interior, were home to a huge number of Mosasaurs, such as Clidastes, Globidens, Halisaurus, Mosasaurus, Prognathodon, Plioplatecarpines and Tylosaurines. However, Mosasaurus was more abundant in the northern Western Interior, while Globidens and Halisaurus were more commonly found in the Gulf of Mexico.

The Western Canadian provinces have produced a vast array of Mosasaur fossils that represents this incredibly diverse community. One particularly impressive site is an ammolite gemstone mining operation in Southeastern Alberta. Now, this area is mined for the shells of Ammonites that are uniquely and beautifully preserved with brilliant opalescent rainbow hues. Of course, Mosasaurs are known to have eaten Ammonites, and the environmental conditions that preserve the vivid colors in the Ammonites' shells also preserved the Mosasaurs in great detail. In fact, even some cartilaginous structures, like the trachea, can be found preserved.

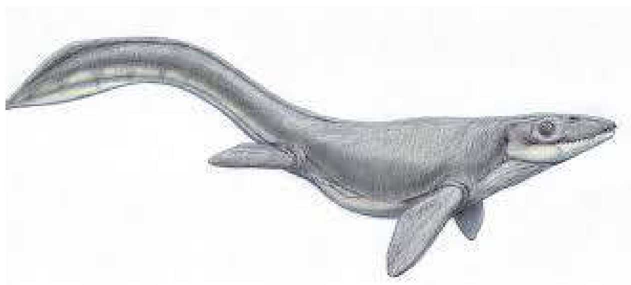


Illustration 120: *Dollosaurus* (Life reconstruction)

Another major community of Mosasaurs has been found in the broadening Atlantic Ocean, from the East coast of North America to the remnants of the Tethys. The fact that the same species of Mosasaurus lived on both sides of the Atlantic, indicates that the deep Ocean did not inhibit the migration of these derived forms. One exception to this is *Dollosaurus*, a Prognathodontine that was unique to Europe at this time.

Illustration 121: *Kourisodon* (Life reconstruction)

The Mosasaur fauna around the Pacific was slightly different, though the genera there are likely closely related to the more familiar groups from North American and Europe. Some unique Pacific genera include *Kourisodon*, which is known from Western Canada and Japan; and the New Zealand taxa Taniwhasaurus, a Tylosaurine, and *Moanasaurus*, which is related to Mosasaurus.

By the Maastrichtian, the Sauropterygians while abundant were less diverse than during their Jurassic heyday. The Mosasaurs, on the other hand, were more diverse and derived than every before, and lived all around the globe. In fact, Mosasaur fossils have been found in Maastrichtian strata from all seven continents, Platecarpines have been found in these locations, giant Tylosaurines here, and diverse though not as aquatically adapted Halisaurines can also be found the World over.

Prognathodontines were nearly everywhere, and Globidens had a new relative called Carinodens. In addition to being more diverse, Mosasaurs were also increasing in size. ***Mosasaurus*** had spread out of the Western Interior, and some specimens from the East Coast of North America and the Netherlands were truly massive. Even though complete fossils of these behemoths have yet to be found, it is estimated that they could easily have exceeded 18 m.

There are a few localities where some unique genera are found. *Plesiotylosaurus* and the Ichthyosaur-like *Plotosaurus*, which are both Mosasaurians, are only found in California. Two unique African specimens come from yet another transcontinental seaway called the Trans-Saharan seaway, which bisected the African continent. Along with the other more common Mosasaurs found in Niger and Nigeria, are unique species called *Pluridens walakeri* and *Goronyosaurus nigeriensis*. *Pluridens* had twice as many teeth as any other Mosasaur. Their thin, cone-like morphology could have formed a basket to catch small Fish and soft invertebrates.

Illustration 122: *Goronyosaurus nigeriensis* (Fossil))

Goronyosaurus, whose relationship to other groups is still unclear, has an unusual skull with small orbits, a blunt snout and large anterior teeth. In some ways, it rather resembles a Crocodile. Goronyosaurus is not found in marine strata, but is actually from sediments deposited by a freshwater river. Perhaps the broad snout supported additional pressure sensors to help it find prey in murky water at the bottom of rivers. In Canada, even though the Maastrichtian age deposits are not as extensive as Campanian rock layers, numerous specimens of Plioplatecarpus have been found across the west. These Canadian Plioplatecarpines show a pattern that is reflected all around the World.

At the end of the Cretaceous, shortly before their extinction, Mosasaurs were not in a state of decline. In fact, the opposite seems to be true. Mosasaurs as a general trend were increasing in size, abundance, diversity, disparity. Then suddenly, they were extinct. The abrupt end of the Mesozoic, brought on by the Cretaceous-Paleogene extinction event, which occurred 66,000,000 y, cut short a lineage that showed no signs of slowing down. The Cretaceous–Paleogene extinction event, also known as the Cretaceous-Tertiary extinction, was a mass extinction of some three quarters of plant and animal species on Earth, including all non-avian Dinosaurs. It occurred over a geologically short period of time, 66,000,000 y ago.

From the moment that the grand animal de Maastricht was unearthed from a mine in 1770, Mosasaurs have been among the most intriguing of prehistoric animals. Descended from terrestrial Lizards, Mosasaurs quickly developed more and more specialized aquatic morphologies, allowing them to dominate marine environments and colonize the Oceans and waterways of the World. Some reached enormous sizes, and with their flexible jaws and powerful teeth they became apex predators. Others lurked in the shallows ready to ambush anything that swam by, and others developed heavy rounded teeth that enabled them to crush the thick shells of invertebrates. All of them were big, fast and dangerous to the other Mesozoic marine life. They were among the largest and most powerful carnivorous animals that ever lived. They dominated the World's Oceans and inland seas for 30,000,000 y, and then with the Cretaceous-Paleogene extinction event, they abruptly vanished. By then, the Ichthyosaurs were long gone, and the Plesiosaurs were in decline. Therefore, the passing of the Mosasaurs marks the end of an era when Reptiles ruled the seas.

3 Conclusions

Throughout the history of marine life, many unrelated groups of Amniotes have converged on similar adaptations in order to live in aquatic environments. We will never know why specifically the first Reptiles returned to the Oceans, but we do know that they started a trend that has continued to the present day. Mesosaurs were the first group of Reptiles to re-enter the water and were followed by many others, including Ichthyopterygians, Sauropterygians and the Mosasauroids. All groups acquired or reacquired profound adaptive modifications that enabled them to engage in an aquatic lifestyle. Giving birth to live young allowed each of them to abandon completely the land, adapting instead to the pressures and challenges of the aquatic environment.

Repeatedly, we see similar solutions to the eight aspects of the aquatic problem that we discussed at the start of this course. Adaptations for propulsion in the water fall under two main categories, broad flippers for appendicular swimming, and a compressed tail or fluke in axial swimmers. Flippers and fins confer stability in a 3D-environment and allow changes in direction. The development of a fusiform, hydrodynamically advantageous shape solves the problem of inertial drag, and a slick exterior surface that would pass smoothly through the water counteracted viscous drag.

Since all secondarily aquatic Amniotes retained air-breathing lungs, their nares migrated to the top of their heads to enable easier breathing. The additional buoyancy created by breathing air was counteracted in a number of ways by increasing body density.

Pachyostosis and osteosclerosis altered the skeleton to increase weight, and, in some cases, Gastroliths performed the same task. Maintaining a constant water and salt balance could have been helped by the development of a salt gland.

Metabolism was a trickier problem, probably solved by a combination of factors such as size, enzymes, lifestyle, and habitat. Vision and hearing were modified for life and a medium that transmits sound well and light poorly. Other adaptations allowed these creatures to take advantage of a completely new ecosystem and set of prey. The jaws of some grew long and narrow, and were filled with pointy teeth to gobble up slippery Fish and Squid. Others grew powerful skulls to kill preys larger than themselves. Still others grew exceptionally long necks that enabled them to snatch Fish 10 m away. The support that the water provided allowed members in each of these groups to grow extraordinarily large, some becoming among the largest aquatic predators ever to inhabit the seas.

Like so many large and diverse groups of ancient animals, the Ichthyopterygians, Sauropterygians and Mosasauroids are gone, extinct by the end of the Cretaceous, leaving no descendants. Just as the terrestrial Dinosaurs dominated the land and the flying Reptiles dominated the skies, the marine Reptiles were the lords of the aquatic realm. These animals may all be long gone, but the allure of their fossils still lives in our imaginations to this day.

You have now reached the end of the 'University of Alberta's MOOC on marine Reptiles. We hope you enjoyed your experience and be sure to investigate our other MOOCs.

Appendix

1 List of Illustrations